

River restorations

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Morphological effects on colonization and succession of aquatic and riparian organism groups

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1 General introduction

Natural rivers and their floodplains are characterized by a high number of various habitat features comprising lotic, lentic, riparian and groundwater areas and including a high diversity of successional stages. The natural disturbance regime of flooding is the main driver for these complex and dynamic systems (Ward et al., 2002). Discharge patterns determine erosion, transport and deposition of bed material and, consequently, the channel form (Hughes, 1997; Ward et al., 2002). Beyond extreme floods, the bankfull discharge, which has a recurrence interval of approximately 1 year, is a key factor influencing riparian and aquatic habitats (Lenzi et al., 2006; Surian et al., 2009), and associated biota and functions (Ward et al., 1999; Pedroli et al., 2002; Jansson et al., 2007). The resulting mosaic of floodplain habitats is unstable and shifts constantly (Ward et al., 1999; Robinson et al., 2002).

High spatio-temporal heterogeneity of habitats due to morphological processes of sediment relocation turns them into hot spots of species, genetic and functional diversity of flora and fauna (Ward et al., 1999; Tockner et al., 2009). This biodiversity comprises various aquatic, amphibious and terrestrial species (Robinson et al., 2002) well adapted to changing habitat conditions or specialized to habitat features, e.g., secondary channels, standing water bodies and dynamic riparian areas.

Aquatic floodplain habitats such as secondary channels, backwaters and ponds are highly important for several organism groups. For example, fish species use these areas for feeding, spawning and nursery (Aarts et al., 2004). Moreover, they provide shelter from predation and the impact of strong flooding events (Schiemer, 2000). Aquatic organism groups, e.g., fish, benthic invertebrates and aquatic macrophytes include many species with specific habitat preferences due to substrate types on the river bottom, depth and current conditions (Cianfrani et al., 2009; Garcia et al., 2011; Lorenz et al., 2012).

Terrestrial and transient areas in natural floodplains feature high substrate diversity and a lateral gradient of moisture from the shoreline to the top edges of embankment offering various niches for plants, invertebrates, birds and mammals (Robinson et al., 2002). They are characterized by a mosaic of different successional stages from bare areas over sparsely vegetated banks to riparian forests (Ward et al., 2002). Especially transient riparian areas which underlie strong dynamic processes are inhabited by well adapted riparian invertebrates and plants (Den Boer, 1990a; Niemelä, 2001; Blom et al., 1990; Blom & Voesenek, 1996). Riparian fauna and flora are strongly dependent on substrate (Antvogel & Bonn, 2001; Sadler et al., 2004; Eyre, 2006), moisture (Böcker et al., 1983; Luff et al., 1989; Diekmann, 2003; Ellenberg, 1974, 1996) and habitat turnover (Turin & Den Boer, 1988; Robinson et al., 2002).

The lateral connectivity between the river and its floodplain is highly important for various biotic and abiotic functions (Ward & Tockner, 2001) and land-water interactions (Hughes, 1997; Boscaini et al., 2000; Ward et al., 2002; Tockner et al., 2010). It is mandatory for species with complex life cycles including aquatic and terrestrial stages that apply to most aquatic insects and pond-breeding amphibians (Wilbur, 1980; Tockner et al., 2010). Biotic interactions between aquatic and terrestrial organisms built the baseline of complex food webs reflecting the strong functional relationship between the river and its floodplain (Woodward & Hildrew, 2002). Riparian arthropods are an important link for the transfer of aquatic food sources to riparian food webs as they feed on benthic invertebrates emerging or stranded at the shoreline (Hering & Plachter, 1997; Paetzold et al., 2006).

Providing biodiversity and supporting habitats for stenotopic and, therefore, less common species is only one of the diverse ecosystem functions and services offered by rivers and their floodplains (Tockner et al., 2008). Since the Middle Ages, human beings increasingly altered rivers and their floodplains to benefit from provisioning, regulatory and cultural services, e.g., navigation, waste water treatment and recreation (Millennium Ecosystem Assessment, 2005). Particularly in densely populated areas, such as Central Europe, most rivers have suffered from straightening, bed and bank fixation, the loss of lateral and longitudinal connectivity and altered flow and sediment regimes. In lentic aquatic ecosystems, nutrient reduction is still the prime restoration target (Jeppesen et al., 2005; Duarte et al., 2009). For rivers and their floodplains in Europe, however, hydromorphological restoration is now the pivotal measure, as pollution with nutrients and organic substances has been drastically reduced over the last several decades. In Germany, only 34% of the river stretches are still polluted with organic substances (BMU, 2010). With cleaner water, it is increasingly apparent that sediment input, water abstraction and habitat modification are widespread pressures affecting functionality and species assemblages of rivers. A nationwide survey in Germany revealed that two thirds of the rivers are morphologically degraded with likely effects on the biota (BMU, 2010). The status of floodplains is still worse as 90% of German floodplains were altered for agricultural landuse, protection of settlements against flooding and alteration of rivers for navigation (BMU & BfN, 2009).

The Water Framework Directive (WFD; Directive 2000/60/EC) established in 2000 aims to improve the ecological status of all ground and surface waters in the European Union according to chemical, hydromorphological and biological conditions. Rivers should be restored to healthy river ecosystems in terms of the good ecological status until 2015 assessed by

characterizing assemblages of fish, benthic invertebrates and aquatic flora (Hering et al., 2010). All River Basin Management Plans drafted in Europe to implement the EU Water Framework Directive rank the improvement of river hydromorphology as one of the top measures (EEA, 2012). In Germany such measures have also been commonly implemented in the past. In example, more than 1,400 measures had been conducted in three Federal States of Germany until 2005 (Feld et al., 2005) and the number still increases. In 2012, 16% of German river stretches were restored due to the requirements of the WFD and 56 % are in the planning or construction phase (BMU, 2013). The vast majority of these measures acts at the site or reach scales; catchment-scale measures are an exception, although large-scale pressures, e.g., catchment land use, often inhibit the success of restoration (Kail & Wolter, 2013).

The term ‘hydromorphological restoration’ covers a diverse suite of measures including the removal of weirs to increase connectivity, the removal of bank fixations and the re-establishment of riparian forest, providing more space for the river.

Restoring the hydromorphology of a short river section does not necessarily yield strong effects on the aquatic biota. There is overwhelming evidence for minor effects on benthic invertebrates (Roni et al., 2006; Jähnig et al., 2010; Palmer et al., 2010), while there are mixed effects on fish (Lepori et al., 2005; Cianfrani et al., 2009; Poff & Zimmermann, 2010) and macrophytes (Pedersen et al., 2007; Lorenz et al., 2012). The reasons for failed restoration success are complex and contain multiple and often catchment-related stressors acting on the restored reach, e.g., agricultural land use and poor water quality (Palmer et al., 2010; Lorenz & Feld, 2013; Sundermann et al., 2013). Other factors, e.g., the length of restored sections, the presence of source populations and time spans required for recolonization are still in discussion to influence the success of restoration. It is criticized that restoration measures on short sections are less sufficient for positive changes in benthic invertebrate compositions (Jähnig et al., 2010; Haase et al., 2013). For fishes and benthic invertebrates, the presence of source populations in the immediate surroundings of the restored sections is an important factor determining recolonization (Stoll et al., 2013; Sundermann et al., 2011b). Some authors (Lorenz et al., 2009; Bernhardt & Palmer, 2011; Parkyn & Smith, 2011) discuss the factor time and suggest that recolonization of restored sections by aquatic organism groups reveals longer time spans than expected. However, studies of restoration effectiveness addressing the factor time are rare.

Due to the requirements of the Water Framework Directive (WFD), restoration measures are assessed exclusively based on their effects on aquatic biota ignoring potentially benefits for

river functionality and riparian communities, although the importance of riparian areas and wetlands for aquatic ecosystems is mentioned in article 1 of the WFD. Almost all measures targeting river hydromorphology simultaneously affect a river's direct surroundings; e.g., by enabling inundations of the riparian zone, increasing morphodynamics, generating riparian habitats such as gravel bars and floodplain ponds and, in general, by better connecting rivers to floodplains. Riparian flora and fauna have the potential to react more rapidly and more strongly to habitat improvement than aquatic communities as both are strongly dependent microclimatic conditions in the floodplain and less on water quality. Several studies addressing individual restoration measures lend support to the conjecture that riparian communities strongly respond to improved habitat conditions (Tockner et al., 1998; Günther & Assmann 2005; Rohde et al., 2005; Lambeets et al., 2008a; Jähnig et al., 2009; Meyer et al., 2010).

The interest of European governments in floodplain restoration increased in recent years (Gumiero et al., 2013). Catastrophic flood events became more frequent in the last decades with negative economic and social effects resulting from channelized river channels and the lack of floodplains (http://ec.europa.eu/environment/water/flood_risk/). The Flood Risk Management Directive (2007/60/EC) established in 2007 demand the assessment of flood risks in all water courses and coastal lines from the European member states and aims at the improvement of flood management plans. Nowadays, European country-led initiatives focusing on floodplains, e.g., 'Living rivers' or 'Room for the river' are accelerating (EEA, 2012). Moreover, there is an increasing number of EU funded LIFE projects which aim to improve river dynamics and reconnect floodplains. However, studies addressing restoration effects on riparian organism groups are rare and standardized assessment methods are still missing. Altogether, the assessment of river ecosystems strongly focusses on aquatic organism groups and ignores the importance of intact floodplains. Furthermore, there is a lack of knowledge about the relevance of the factor time for restoration success. This leads to the following questions:

- (1) How do riparian organism groups respond to hydromorphological restoration measures?
- (2) How do habitats and species assemblages of the river and the floodplain develop in the first years after restoration and over time?
- (3) How do aquatic and riparian organism groups differ in their response to restoration measures?

Scope of this thesis

The objective of this thesis is to shed light on morphological and biological responses of rivers and their floodplains to restoration measures.

First, effects of hydromorphological restoration on riparian habitats and organism groups were analyzed by using the example of carabid beetles and floodplain vegetation for a dataset of 24 restoration measures (chapter 3). Second, successional processes in different time scales were considered in comparison of restoration effects on aquatic and riparian habitats and several organism groups (chapter 4 and 5). The analyses addressing the factor time were based on two case studies of mid-sized mountain rivers investigated at different time periods after restoration. In detail, the following hypotheses are tested:

- (1) *Richness and diversity of habitats and species in riparian areas is higher in restored than in non-restored sections (chapter 3).*

Restoration creates a diverse array of riparian habitats, e.g., bars, islands and flood-prone areas which support colonization of diverse and species-rich plant and carabid assemblages. Pioneer species and hygrophilous species benefit strongest from habitat changes as they are adapted to dynamic riparian areas and flooding.

- (2) *The time since restoration influences habitats and species assemblages in aquatic and riparian areas (chapter 4 and 5).*

- a) *Riparian pioneer species and species with high dispersal ability colonize restorations immediately after construction works, whereas aquatic organism groups require longer time spans for developing near-natural assemblages (chapter 4).*

In the first years after restoration, sections offer virgin habitats as a starting point for pioneer colonization. After a time period of 18 to 20, restored sections are colonized by riparian pioneers and competitive species and by aquatic species with comparatively lower dispersal ability.

- b) *Habitat heterogeneity in aquatic and riparian areas of restored sections is maintained by dynamic processes, which is enabled by restoration, and increase species richness in the long-term (chapter 5).*

The removal of bank fixations and the creation of shallow transient areas enable dynamic processes in terms of sediment relocation in the river bottom and in riparian zones. Due to flooding events, normally occurring in winter and spring, dynamic processes maintain habitat heterogeneity in aquatic and riparian areas in the long-term. This enables constant colonization of habitats by aquatic and riparian species which enriches of the local species pool.

(3) *The magnitude of responses to restoration differs between aquatic and riparian organism groups (chapter 4 and 5).*

Stronger responses of riparian organism groups result from higher dispersal abilities compared to aquatic organism groups. Riparian carabid beetles disperse actively by flying. Floodplain vegetation has various passive dispersal strategies, e.g., hydrochory, anemochory and zoochory, and reproduce from the soil seed bank. Minor responses of aquatic organism groups to restoration result from lower dispersal ability, as their dispersal is strongly bound to the aquatic pathway and the river corridor and affected by multiple stressors.

2 Field work and data preparation

All analyses aimed to quantify restoration effects. Therefore, we compared non-restored and nearby restored sample sections (control-impact design) as data from before the implementation of restoration measures were mostly missing. Non-restored sections reflected the condition before the implementation of measures and were located up to 500 m upstream from restored sections. Therefore, the paired restored and non-restored sections were almost similar in terms of catchment land use, river size and slope.

2.1 Morphology

For morphological surveys, we observed sample sections with a length of 100 m in case of small rivers (catchment size $< 100 \text{ km}^2$) and 200 m in case of mid-sized rivers (catchment size $100\text{-}1,000 \text{ km}^2$). We divided each section into ten transects with an equal distance of 10 m respectively 20 m spanning the area between the top edges of the embankment (Figure 2-1).



Figure 2-1: Sample section divided into ten transects using the example of the restored section of Lahn Cölbe; black lines = location of transects (picture was taken by A. Lorenz in April 2009).

2.1.1 Mesohabitats

We surveyed aquatic and riparian mesohabitats (Table 2-1) partly based on Raven et al. (1997) and Jähnig et al. (2008) in summer at low flow conditions. We recorded their lengths along the ten transects per sample section. For chapter 4, we used a finer classification of riparian mesohabitats, as we aimed at analyses of successional patterns in riparian zones, e.g., changes in herbaceous and woody banks.

Table 2-1: Recorded aquatic and riparian mesohabitats and descriptions; modified after Raven et al. (1997) and Jähnig et al. (2008).

	Mesohabitats analyzed in chapter 3 and 5	Mesohabitats analyzed in chapter 4	Description
Aquatic area	Main channel	Main channel	Hydrological dynamic water body, most important runoff channel
	Secondary channel	Secondary channel	Hydrological dynamic water body, connected with the main channel at both ends, less water runoff
	Connected sidearm	Connected sidearm	Water bodies lacking unidirectional current, connected only at the downstream or upstream end
	Disconnected sidearm	Disconnected sidearm	No connectivity with the main channel
	Permanent standing water body	Permanent standing water body	On the floodplains, fed by high water levels and groundwater, no signs of drying
	Temporary standing water body	Temporary standing water body	On the floodplains, fed by high water levels, will dry out quite shortly, puddle-like
Riparian area	Bank	Bank with woody vegetation	Woody aquatic-terrestrial transient zone with an inclination $< 30^\circ$
		Bank with herbaceous vegetation	Herbaceous aquatic-terrestrial transient zone with an inclination $< 30^\circ$
	Unvegetated bar	Unvegetated bar	Unvegetated bar close-by the shoreline either at the floodplain or at an island; bar in the middle of main or secondary channel
	Vegetated island	Island with woody vegetation	Large bar with woody vegetation, separating main and secondary channel(s)
		Island with herbaceous vegetation	Large bar with herbaceous vegetation, separating main and secondary channel(s)
	Embankment	Artificial embankment	Artificially created zone e.g. with trapezoidal or rectangular profile, often built of blocks as bank fixation
		Embankment with woody vegetation	Riparian zone with woody vegetation and an inclination $> 30^\circ$, confines bankfull discharge area
		Embankment with herbaceous vegetation	Riparian zone with herbaceous vegetation and an inclination $> 30^\circ$, confines bankfull discharge area
	Eroding cliff	Eroding cliff	Vertical, near vertical or undercut bankface profile with an inclination $> 50^\circ$; if inclination is 90° , length = 0
	Floodplain area	Floodplain area	Zone within the bankfull discharge area, which is prone to flooding and characterized by high humidity

2.1.2 Microhabitats

In each sample section, we recorded microhabitats (Table 2-2) in terms of substrate types (compare Hering et al., 2003) on the river bottom at ten points per transect resulting in 100 point data per section. For analyses in chapter 4, we additionally recorded riparian microhabitats and their length along the ten transects.

Table 2-2: Microhabitat classification and description based on substrate types according to multi-habitat sampling protocol (Hering et al., 2003); substrates marked grey were also recorded for analyses of riparian microhabitats in chapter 4.

Microhabitat	Description	Type	Grain size [mm]
Macrolithal and technolithal	Large cobbles, boulders and blocks, bedrock; coarse blocks, head-sized cobbles, with a variable percentages of cobble, gravel and sand; in our river sections mainly artificial (= technolithal)	mineral	> 200
Mesolithal	Fist to hand-sized cobbles with a variable percentage of gravel and sand	mineral	> 60-200
Microlithal	Coarse gravel (size of a pigeon egg to child's fist) with variable percentages of medium to fine gravel	mineral	> 20-60
Akal	Fine to medium-sized gravel	mineral	> 2-20
Psammal	Sand	mineral	> 0.006–2
Argyllal	Silt, loam, clay (inorganic)	mineral	< 0.006
Xylal	Tree trunks, dead wood, branches, roots	biotic	
CPOM	Deposits of coarse particulate organic matter, e.g., fallen leaves	biotic	
FPOM	Deposits of fine particulate organic matter, e.g., mud und sludge (organic)	biotic	
Algae	Filamentous algae, algal tufts	biotic	
Submerged macrophytes	Submerged macrophytes, including moss and Characeae	biotic	
Emergent macrophytes	Emergent macrophytes, e.g., <i>Typha</i> , <i>Carex</i> , <i>Phragmites</i>	biotic	
LPTP	Living parts of terrestrial plants, e.g. fine roots, floating riparian vegetation	biotic	
Xylal	Dead wood and tree trunks	biotic	

We aimed for comparable data of habitat composition for micro- and mesohabitats. Therefore, we calculated the proportions of instream microhabitats (PX_{sample}) and floodplain mesohabitats (PY_{sample}) for each sample based on the microhabitat data points and on the lengths of mesohabitats along ten transects:

$PX_{\text{sample}} = \frac{\text{number of data points with microhabitat X}}{\text{total number of data points}}$, whereas the total number of data points per sample was 100,

and

$$PY_{\text{sample}} = \left(\frac{\text{total length of mesohabitat Y}}{\text{total length of all mesohabitats}} \right) * 100.$$

2.2 Organism groups

2.2.1 Riparian organism groups

The investigations of riparian organism groups, which built the baseline for each chapter of the thesis, were based on the following sample methods.

Floodplain vegetation was surveyed in late summer on a 2 m wide strip along three transects located at the upper, middle and lower area of each sample section. We classified vegetation units according to Oberdorfer (1983, 1992) and Ellenberg (1996) and measured their lengths along transects. We calculated the proportion of units per sample section and used this value as a proxy for extension. For all vegetation units present in the three transects, we recorded plant species on three 2 x 3 m sampling spots. The coverage of all species was estimated using the following abundance classes: 1%, 5%, 10%, 15%, 20% and continuing in 10%-steps up to 100%.

For carabid beetle sampling, three transects were randomly selected. We used a combination of pitfall trap (Barber, 1931) and hand collection (Trautner, 1992, 1999) techniques once per sample section in the midst of summer (June to July). We installed traps (4 cm diameter, 8.5 cm depth, 200 ml volume), filled with 100 ml Renner-solution (Renner 1980) and a detergent to reduce surface tension, in predominantly vegetated mesohabitats; i.e., 1-3 traps set per transect according to the number of vegetated mesohabitats. Traps were exposed for one week and protected from rain by petri dishes. We performed up to six hand collections per sample section at bare mesohabitats (e.g., bars) dependent on the frequency and extent of these habitats on the three transects. For each hand collection, we sampled carabid beetles with an exhaustor on an area of 1 m². After driving out beetles hidden in the sediment by inundation, we

scanned the area for a maximum of twenty minutes by turning stones and organic substrates. We transferred all beetles into ethyl alcohol (70%) and identified them to species level according to Müller-Motzfeld (2004).

For plants and carabids, quantitative taxalists per section were generated by the following procedure of habitat-weighting.

First, we calculated mean abundances of plant (M_p) and carabid (M_c) species per habitat (based on vegetation units for plants and on floodplain mesohabitats for carabids) for each sample separately.

For plant species, we calculated the area A_s in m^2 that is covered by plant species x for each of the three sample spot recorded per vegetation unit separately:

$$A_s = \frac{\text{Coverage of species } x \text{ in one sample plot}}{100} * 6m^2.$$

Then we calculated the mean coverage M_p in the three sample plots which exhibits the average abundance of plant species x per vegetation unit:

$$M_p = \frac{(As1 + As2 + As3)}{3}.$$

For carabid beetles, the mean abundance of each species y in mesohabitat m (M_c) was calculated by summing up the number of individuals within each mesohabitat and dividing it by the number of sampled mesohabitats.

Second, to upscale species abundances on the sample section, we calculated habitat-weighted mean abundances for each plant (H_p) and carabid species (H_c). Therefore, we multiplied the mean abundances of each plant (M_p) and carabid (M_c) species with the proportion of the respective habitats. The abundances per habitat given as proportions were calculated from the lengths of vegetation units along transects (floodplain vegetation) and from the length of floodplain mesohabitats along transects (carabid beetles):

$$H_p = M_p * 100 * \left(\frac{\text{total length of vegetation unit } v}{\text{total length of all vegetation units}} \right),$$

$$H_c = M_c * 100 * \left(\frac{\text{total length of mesohabitat } m}{\text{total length of all mesohabitats}} \right).$$

At least, we summed up the habitat-weighted abundances per habitat for each species and sample.

2.2.2 Aquatic organism groups

The investigations of aquatic organism groups comprised benthic invertebrates (chapter 4 and 5), aquatic macrophytes (chapter 4) and fish (chapter 4).

Benthic invertebrates were sampled in June/July as recommended for midsized rivers (catchment of 100-1,000 km²) using a multihabitat-sampling design (Meier et al., 2006). We took 20 sample units per river section whereas the substrates were sampled according to their proportional presence in the section using a shovel sampler (25 x 25 cm; 500 µm mesh size). The sample material (20 sample units per section together) was preserved with ethanol (96%) and sorted according to Haase et al. (2004). Species were identified to the lowest possible level as suggested by Haase et al. (2006) and quoted as individuals per m² for each sample.

Aquatic macrophytes were surveyed in late summer by using the German standard method (Schaumburg et al., 2004, compare also Lorenz et al., 2012). All submerged, free-floating, amphibious and emergent angiosperms, liverworts and mosses were recorded by wading in a zigzag manner across the channel and walking along the riverbank. Furthermore, plants which were attached or rooted in parts on the river bank and submerged for more than 85% of the year were recorded. In non-wadeable areas, a rake was used to reach the macrophytes on the river bottom. Identification of macrophytes was done at the species level, except for *Callitriche* stands without fruits; for these, identification stopped at the genus level. The frequency and abundance of each species was estimated using the 5-point scale given by Kohler (1978): 1 = very rare, 2 = rare, 3 = common, 4 = frequent, 5 = abundant, predominant. Values of the 5-point scale were transformed by using the function $y = x^3$ according to Kohler & Janauer (1997) and Schaumburg et al. (2004) to get quantitative data.

Fishes were investigated in early autumn according to the German guidelines devised by Diekmann et al. (2005). Electrofishing was done by boat on section lengths 100 times the river width and as single passes with a generator-powered DC electric fishing gear. Riparian areas were fished upstream (3 m on the left and right bankside zone) and the middle of the river was fished downstream. For identification and length measurements, all collected fishes were stored in a container. When sampling was finished, they were brought back into the river. Species in taxalists were classified in young-of-the-year and adult individuals. We transformed abundances of species to individuals per hectare.

3 Effects of river restorations on riparian mesohabitats, floodplain vegetation and carabid beetles

3.1 Introduction

The riparian zone of rivers is characterized by a diverse and highly specialized vegetation and fauna strongly adapted to flooding disturbance and habitat turnover. River banks are typically colonized by pioneer plants (Tabacchi et al., 1998; Gilvear & Willby, 2006) and by specialized, mostly full-winged carabid beetles capable of rapidly colonizing new banks generated by floods (Sadler et al., 2004, Lambeets et al., 2009). In the past, these assemblages have strongly been affected by channelization and altered flow regimes (Greenwood et al., 1991, Godreau et al., 1999, Tockner et al., 2008). Since centuries, ‘anthropogenic disturbance’ increasingly altered river systems for e.g., agricultural and industrial purposes and for flood protection (Naiman et al., 2005). Flow regulation as the most important threat for rivers and their riparian zones leads to alteration of sediment transport, reduction of flood peaks, flooding frequency and channel forming flows (Naiman et al., 2005). The resultant ‘terrestrialization’ affects physical (e.g. erosion and deposition of sediment that naturally forms channel morphology) and ecological functions (e.g. nutrient buffers, refuges for regional diversity, longitudinal pathways) impoverishing the complex array of life-history strategies and successional patterns (Naiman & Décamps, 1997). Riparian biota might therefore benefit from the reversal of degradation by hydromorphological restoration. There are few studies lending support to the conjecture that restoration promotes plant richness and diversity (Andersson et al., 2000; Baattrup-Pedersen et al., 2000; Jähnig et al. 2009a), carabid species richness (Lambeets et al., 2008a, Jähnig et al., 2009a) and the occurrence of stenotopic carabids (Günther & Assmann, 2005). However, as these studies address single or only a few reaches, they do not allow for a generalization of restoration effects on riparian assemblages.

In this study, we compare the effects of restoration on riparian mesohabitats, floodplain vegetation and carabid beetles using a control-impact design in the riparian zones of 24 restored rivers in Germany. More specifically, we hypothesize that, independent of the time since restoration, hydromorphological restoration initiates a general increase of:

- richness and diversity of riparian mesohabitats, vegetation and carabid beetles,
- taxonomic diversity of plant and carabid species,
- stress-tolerant pioneers of plant and carabid species,
- hygrophilous plant and carabid species.

We analyzed differences in these variables for species assemblages of restored versus non-restored sample sections. The frequency and intensity of restoration effects were analyzed by the number and amount of site-specific changes.

3.2 Sample sections and field work

3.2.1 Sample sections

We sampled 24 study sites in mountainous and lowland regions in Germany (Figure 3-1, Table 3-1). Germany belongs to the temperate zone and is located in the transition region between the maritime climate in Western Europe and the continental climate in Eastern Europe. The mean annual temperature in Germany is 8.6° C (1971-2000), varying from a monthly average of 0.2° C in January to 17.4° C in July (DWD, 2010); average temperature in 2008 was 10.5 % above this mean value. Precipitation, existent throughout the whole year with an average of 787 mm/year (1971-2000), varies from a monthly average of 48 mm in February and 83 mm in June; average precipitation in 2008 was 1.1 % below this mean value (DWD, 2010).

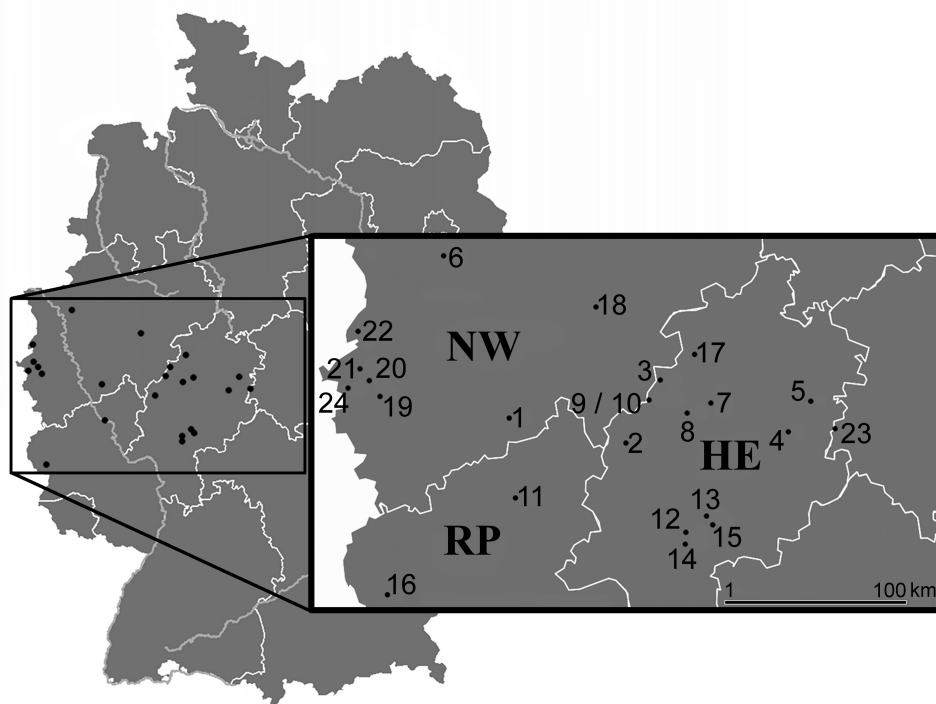


Figure 3-1: Location of the 24 study sites in Germany; site numbers according to table 3-1; NW: North Rhine-Westphalia, RP: Rhineland-Palatinate, HE: Hesse.

A study site comprised a restored and a non-restored sample section with a length of 100 m in case of small rivers (catchment size $< 100 \text{ km}^2$) and 200 m in case of mid-sized rivers (catchment size $100\text{--}1,000 \text{ km}^2$). Non-restored sections were located up to 500 m upstream from restored sections, so the paired restored and non-restored sections were similar in terms of catchment land use, river size and slope. For mountain rivers, catchment land cover was mainly forest with agricultural areas and settlements restricted to the floodplains, while in lowland catchments agricultural land use predominated. Rivers were restored 1 and 14 years prior to the investigation (median 5 years) with the length of restored river sections varying from 200 to 2,500 m (Table 3-1). Restoration measures included removal of bank reinforcement, increase of flooding areas resulting from lowering of entrenchment depth and active digging of flooding areas at water level, extensification of landuse and recreation of flood-prone riparian areas resulting from the creation of new water courses and secondary channels.

3.2.2 Field work

We investigated riparian mesohabitats, floodplain vegetation and carabid beetles in 21 study sites once in June and July 2008. For three additional sites (Lahn Cölbe, Lahn Ludwigshütte and Lahn Wallau), we used data collected by Jähnig et al. (2008, 2009a) in 2005 that were recorded with comparable methods.

Riparian mesohabitats were surveyed along ten transects per river section with an equal distance of 20 m spanning the area between the top edges of the embankment. Partly based on Raven et al. (1997) and Jähnig et al. (2008), we recorded riparian mesohabitats and their lengths along transects to determine the proportion of mesohabitats per river section. Detailed descriptions of morphological recording and data preparation are given in chapter 2.1.

Floodplain vegetation and carabid beetles were surveyed using the grab sampling method as described in chapter 2.2. We simplified the more complex vegetation data from Jähnig et al. (2008) to the grab sampling level applied to the other study sites. Detailed descriptions of the sampling procedures and the preparation of taxalists are given in chapter 2.2.

Table 3-1: Study sites, locations and year/type of restoration measure (River type: M = Mountain, L = Lowland).

Site number	River name	Site name	Longitude [decimal, WGS84]	Latitude [decimal, WGS84]	Catchment size [km ²]	River type	Restoration year	Restoration measures			
								Removal of bank fixation	Increase of flooding areas	Extensification of landuse	Recreation of flood-prone riparian areas (banks, bars)
1	Bröl	Waldbröl	7.38466	5.082.645	181	M	1995	–	–	x	x
2	Dill	Dillenburg	8.30873	5.070.855	314	M	2005	–	–	x	x
3	Eder	Dodenau	8.57328	5.102.737	480	M	2000	x	–	x	x
4	Fulda	Mecklar	9.76377	5.091.992	2375	M	2005	–	x	–	x
5	Fulda	Niederaula	9.58281	5.076.640	1290	M	2005	–	x	–	–
6	Gartroper Mühlenbach	Hünxe	6.83010	5.162.783	9	L	2004	x	x	x	x
7	Josbach	Josbach	8.97656	5.091.170	29	M	2003	–	x	x	–
8	Lahn	Cölbe	8.79105	5.086.220	650	M	2000	x	x	x	x
9	Lahn	Ludwigshütte	8.49874	5.092.540	288	M	2002	x	x	–	x
10	Lahn	Wallau	8.48606	5.092.733	278	M	2001	x	x	–	x
11	Nette	Weißenthurm	7.44756	5.043.388	370	M	2007	x	x	x	–
12	Nidda	Ilbenstadt	8.78208	5.026.834	1168	M	2006	x	x	x	x
13	Nidda	Ranstadt	8.93911	5.034.731	226	M	2004	x	–	x	x
14	Nidda	Bad Vilbel	8.77394	5.020.888	1200	M	2001	x	x	x	x
15	Nidder	Altenstadt	8.98851	5.030.493	153	M	2002	x	–	x	x
16	Nims	Birtlingen	6.48411	4.994.746	222	M	2000	–	–	x	–
17	Orke	Niederorke	8.84330	5.115.505	289	M	1998	x	–	x	x
18	Ruhr	Arnsberg	8.05998	5.138.926	1050	M	2004	x	x	x	x
19	Rur	Jülich	6.35099	5.092.219	1335	M	1996	x	–	x	x
20	Rur	Körrenzig	6.27147	5.099.133	1472	L	2001	x	x	x	–
21	Rur	Millich	6.19285	5.104.893	1715	L	2002	x	–	x	x
22	Schwalme	Brüggen	6.16676	5.123.686	319	L	1997	x	–	x	x
23	Ulster	Wenigentaft	9.95376	5.078.054	384	M	2006	x	–	x	x
24	Wurm	Frelenberg	6.10616	5.094.954	251	L	2007	x	x	–	x

3.2.3 Data processing and analyses

Based on quantitative lists of habitats and taxa, we calculated the following 18 indices for each section. Richness indices comprised the total number of mesohabitats and vegetation units along transects as well as the plant and carabid species numbers. The Shannon-Wiener index was calculated for the relative lengths of mesohabitats and vegetation units as well as for the percentaged abundances of plant and carabid species.

Taxonomic diversity Δ (Warwick & Clarke, 1995) of plants and carabids was calculated as:

$$\Delta = \frac{[\sum \sum_{i < j} \omega_{ij} x_i x_j]}{\left[\frac{n(n-1)}{2} \right]},$$

where ($i=1, \dots, s$) is the abundance of the i th species, n ($= \sum_i x_i$) is the total number of individuals in the sample and ω_{ij} is the “distinctness weight” resulting from the path length linking species i and j in the taxonomic classification. The index thus considers species diversity and phylogenetic separation and is based on the average taxonomic distance between any two randomly chosen species.

We calculated ecological strategy indices as the percentaged abundances and numbers of stress-tolerant pioneers of plant (Klotz & Kühn, 2002) and carabid species (Koch, 1989; Gesellschaft für Angewandte Carabidologie, 2009). Transient forms between ruderal and stress-tolerant plant species as well as between ruderal and competitive plant species were also considered stress-tolerant. The former are short-living and adapted to extreme conditions (e.g., wet habitats), whereas the latter are larger-sized, annual hibernating or short-living perennial species. In case of carabid beetles, we considered stenotopic riparian species adapted to unstable habitats and mostly full-winged to be stress-tolerant pioneers. We calculated moisture indices as percentaged abundances and numbers of hygrophilous species. For plants species, we used indicator values according to Ellenberg (1996). Species with moisture indicator values from 7 (dampness indicator) to 10 (indicator of shallow-water sites) were considered hygrophilous. The classification of hygrophilous carabid species was based on Koch (1989) and Gesellschaft für Angewandte Carabidologie (2009).

We first compared the range of values for restored and non-restored sections. Differences between the assemblages of restored and non-restored sections were tested with the Mann–Whitney U-test. We identified potential correlations between index values of restored sections and the age since restoration as well as site-specific morphological conditions with Spearman rank correlation.

Second, we calculated the relative index deviation (= rid) of each section pair for richness ($\text{rid}_{\text{richness}}$):

$$\text{rid}_{\text{richness}} = \frac{(\text{value of restored section})}{(\text{value of non-restored section})},$$

where $\text{rid}_{\text{richness}} > 1$: increased richness

$\text{rid}_{\text{richness}} = 1$: unchanged richness

$\text{rid}_{\text{richness}} < 1$: decreased richness.

For the other indices, this way of calculation was not possible (0-value of non-restored section in some cases), so these were calculated as:

$$\text{rid}_{\text{others}} = (\text{value of restored section}) - (\text{value of non-restored section}),$$

where $\text{rid}_{\text{others}} > 0$: increased index

$\text{rid}_{\text{others}} = 0$: unchanged index

$\text{rid}_{\text{others}} < 0$: decreased index.

We summed up the number of study sites with increased, unchanged or decreased index values to define the frequency of restoration effects for each index and taxonomic group.

Third, we used the values of relative index deviation to compare the amount of site-specific index changes for riparian mesohabitats, vegetation units, plant and carabid species resulting in a generalized statement for which group and index restoration success was highest or lowest.

Overall, we did not split up lowland and mountain river sections and did not correct the data for river size and river type as we aimed at general patterns in responses to restoration. Longitudinal zonation, as it is an important factor for benthic invertebrate assemblages (compare ‘River Continuum Concept’, Vannote et al., 1980), is not a key factor for carabid communities; the latter are mainly determined by the presence or absence of habitat templates (Van Looy et al., 2005).

3.3 Results

3.3.1 Comparison of restored and non-restored sections

12 of 18 indices were significantly higher in restored sections (Figure 3-2 and Figure 3-3). Richness and diversity increased for all groups (mesohabitats, vegetation units, plant and carabid species) except carabid diversity (Figure 3-2). Taxonomic diversity of carabid species

was lower in restored sections whereas there were no differences between restored and non-restored sections for the plants. Functional indices according to stress-tolerant pioneers were significantly higher in restored river sections for both plants and carabids (Figure 3-3); the increase was particularly high for carabids with a percentage of up to 90%. Indices according to moisture (abundance and number of hygrophilous plant and carabid species) strongly varied within both non-restored and restored river sections while the median did not differ. Restored sections were generally characterized by a high coverage of the vegetation units Phalaridion and Aegopodion, the plant species *Carex acutiformis* and *Salix fragilis* and frequent occurrences of the carabid species *Bembidion decorum* and *B. tibiale*; these species were also present in non-restored sites but in lower abundances. 20 of 37 vegetation units (e.g., vegetation of open gravel bars such as Therio-Airion, Dauco-Melilotion and Alysso-Sedion; Agropyro-Rumicion) and 175 of 418 plant species (e.g., *Veronica beccabunga*, *Nasturtium officinale* and *Calamagrostis epigejos*) were restricted to restored sections. For the carabids, 27 of 87 species were only found at restored sections (e.g., *Bembidion atrocaeruleum*, *B. femoratum* and *B. punctulatum*), 10 of which belonged to the genus *Bembidion*.

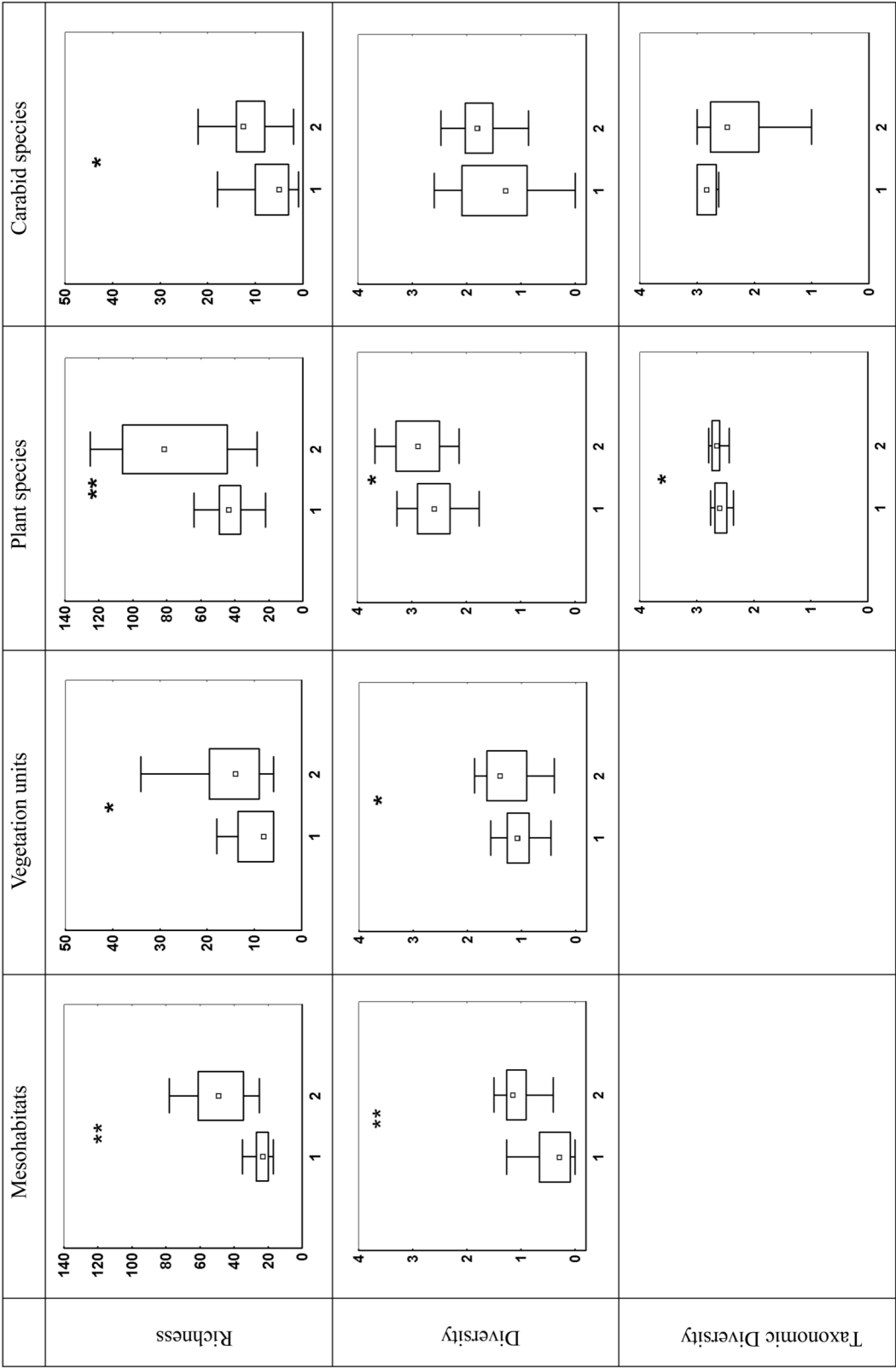


Figure 3-2: Comparison of restored and non-restored sections: indices of richness and diversity (1 = non-restored; 2 = restored); Median, Box: 25-75%, Whisker: non-outlier range; **: significant at $p < 0.01$; *: significant at $p < 0.05$.

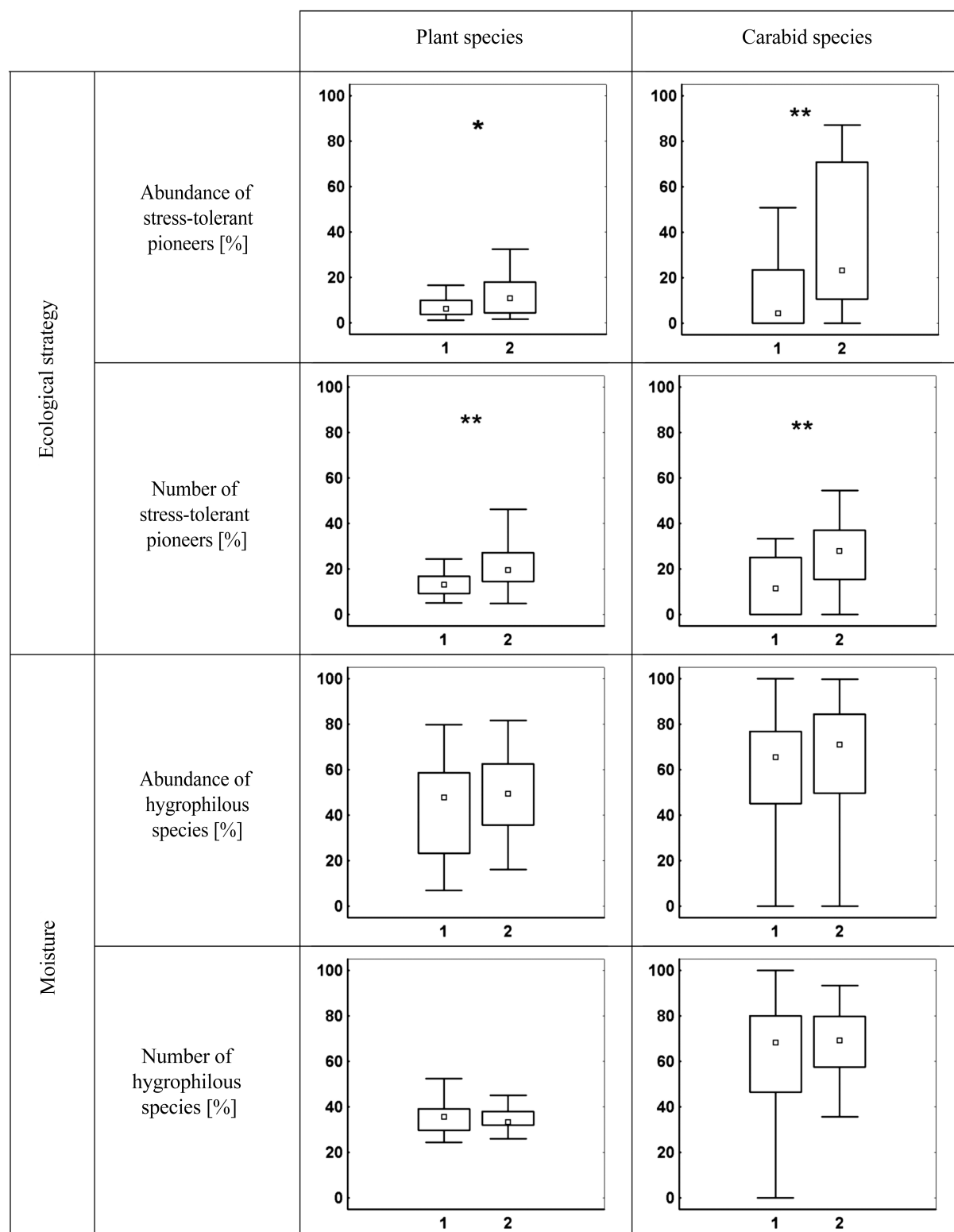


Figure 3-3: Comparison of restored and non-restored sections: functional indices ‘Ecological strategy’ and ‘Moisture’ (1 = non-restored; 2 = restored); Median, Box: 25-75%, Whisker: non-outlier range; **: significant at $p < 0.01$; *: significant at $p < 0.05$.

The time since restoration did not affect plant and carabid indices (Table 3-2). Stress-tolerant pioneer and hygrophilous plant species were more abundant, if richness of riparian mesohabi-

tats was higher. A high diversity of riparian mesohabitats and a high percentage of transient mesohabitats led to increased values of almost all functional indices.

Table 3-2: Temporal and morphological correlations of indices in restored river sections (Spearman rank correlation; ** = significant at $p < 0.01$, * = significant at $p < 0.05$).

		Age since restoration	Richness of riparian mesohabitats	Diversity of riparian mesohabitats	Percentage of transient riparian mesohabitats
Vegetation units	Richness	0.34	0.04	0.05	-0.17
	Diversity	0.14	0.12	0.09	-0.20
Plant species	Richness	0.12	0.08	0.05	0.09
	Diversity	0.18	-0.05	0.01	0.03
	Taxonomic Diversity	0.26	-0.08	0.08	0.20
	Abundance of stress-tolerant pioneers [%]	-0.38	0.53**	0.42	0.23
	Number of stress-tolerant pioneers [%]	-0.19	0.00	0.07	0.25
	Abundance of hygrophilous species [%]	-0.34	0.47*	0.17	-0.05
	Number of hygrophilous species [%]	0.30	0.06	-0.03	-0.20
Carabid species	Richness	0.07	-0.01	-0.13	0.17
	Diversity	0.12	-0.04	-0.17	0.18
	Taxonomic Diversity	0.18	0.08	-0.28	-0.46*
	Abundance of stress-tolerant pioneers [%]	0.03	0.40	0.53**	0.69**
	Number of stress-tolerant pioneers [%]	-0.07	0.27	0.46*	0.60**
	Abundance of hygrophilous species [%]	0.26	0.30	0.44*	0.48*
	Number of hygrophilous species [%]	0.11	0.21	0.27	0.10

3.3.2 Frequency of restoration effects

Richness of riparian mesohabitats increased in all restored sections compared to non-restored sections (Table 3-3), followed by plant species (22), vegetation units (19) and carabid species (17). Patterns of diversity changes were similar, though the frequency of effects was marginally lower. Carabid diversity increased in those restored sections with high habitat diversity including open gravel bars and vegetated mesohabitats and decreased in sparsely colonized sites where non-restored sections were slightly more species-rich. Taxonomic diversity of plant species increased in 15 and declined in 9 restored sections, whereas taxonomic diversity of carabid species increased only in 8 and declined in 16 restored sections.

Table 3-3: Frequency of restoration effects on riparian mesohabitats, vegetation and carabid beetles: counted numbers of increased, unchanged and decreased index values by comparing restored with non-restored sections.

		Riparian meso-habitats	Vegetation units	Plant species	Carabid species
Richness	Increased	24	19	22	17
	Unchanged	0	4	0	1
	Decreased	0	1	2	6
Diversity	Increased	22	17	18	15
	Unchanged	0	0	0	1
	Decreased	2	7	6	8
Taxonomic Diversity	Increased	---	---	15	8
	Unchanged			0	0
	Decreased			9	16
Abundance of stress-tolerant species [%]	Increased	---	---	19	17
	Unchanged			0	2
	Decreased			5	5
Number of stress-tolerant species [%]	Increased	---	---	20	17
	Unchanged			0	2
	Decreased			4	5
Abundance of hygrophilous species [%]	Increased	---	---	15	14
	Unchanged			4	0
	Decreased			5	10
Number of hygrophilous species [%]	Increased	---	---	12	11
	Unchanged			1	2
	Decreased			11	11

Ecological strategy indices increased in most restored sections for both groups, with a decline in only four to five cases. Stress-tolerant carabid species declined only in restored sections with a predominantly vegetated riparian zone and only small patches of open gravel bars. Abundances of hygrophilous plant and carabid species increased in two-thirds of cases, while richness of hygrophilous species increased and decreased in almost similar numbers of sites.

3.3.3 Intensity of restoration success

Here we compared the amount of sites-specific index changes in terms of the values of relative index deviation for each index and group (riparian mesohabitats, vegetation units, plant and carabid species). For all richness indices, the median roughly doubled in restored sections (Figure 3-4). Richness changes of plant species varied only marginally between study sites, whereas the number of carabid species increased in restored sections by factors of 1 to 4.5. The highest changes in median diversity were observed for riparian mesohabitats, with an increase by a value of 0.8. Although overall changes in carabid diversity were lowest, the carabid communities of the individual sites responded differently, including both positive and negative changes in diversity. Most positive changes were found in the study sites ‘Rur Körrenzig’, ‘Schwalm Brüggen’ and ‘Lahn Ludwigshütte’, where restoration resulted in diverse mesohabitats and vegetation patterns. In contrast, carabids in the paired site ‘Dill Dillenburg’, characterized by decreased mesohabitat, vegetation unit and plant diversity, lost most of its carabid diversity. Median taxonomic diversity of plant and carabid species differed only marginally between restored and non-restored sections (higher for plants, lower for carabids), while the variation of carabid taxonomic diversity between sites was high.

Share and number of stress-tolerant pioneers slightly increased, whereas for carabid species both indices increased by approximately 20%, with a maximum increase of 85%. Differences were highest in sites with restored sections characterized by large open gravel bars. Median abundances of hygrophilous plant and carabid species increased by 5 to 10%. These indices had a wide range of positive and negative responses at individual sites; just for some single sites high positive changes could be deduced from the presence of wide floodplain areas (e.g. ‘Gartroper Mühlenbach’ for carabids and ‘Nims Birtlingen’ for plants).

The number of hygrophilous plant and carabid species did not change significantly. Highest restoration success in terms of the amount of site-specific changes were reflected by richness indices for all groups, diversity of riparian mesohabitats and taxonomic diversity, abundance and number of stress-tolerant pioneer species.

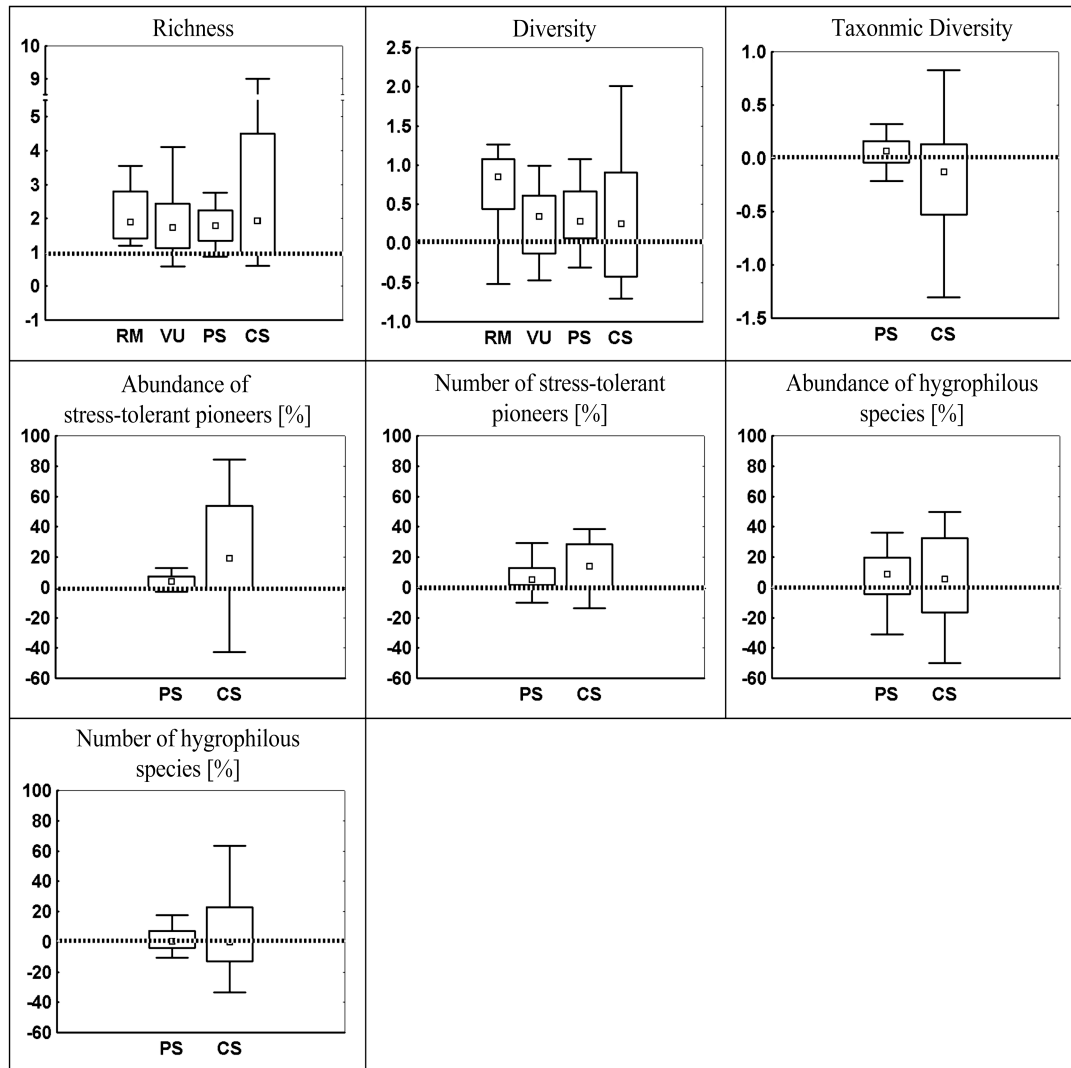


Figure 3-4: Intensity of effects on morphology, floodplain vegetation and carabid beetles based on site-specific restoration success. Parameters: RM = riparian mesohabitats, VU = vegetation units, PS = plant species, CS = carabid species; Median, Box: 25-75%, Whisker: non-outlier range. Open squares = no difference between restored and non-restored sections.

3.4 Discussion

3.4.1 Restoration effects on habitat diversity, species richness and species diversity

Richness measures were generally higher in restored than in non-restored sections. Channel widening and the removal of bank fixations directly affected habitat diversity by generating sand and gravel bars, islands and floodplain ponds. On a smaller scale more frequent inundations of the riparian zones were enabled which diversified microhabitat characteristics further, e.g., substrate and humidity conditions. Our results support the hypothesis that increased beta (habitat) diversity yields higher species numbers and (alpha) diversity, as additional plant communities, plant and carabid species occur independent of the time since restoration. Not necessarily related to restoration, the general importance of habitat diversity and habitat turnover for species-rich riparian plant and carabid assemblages has been highlighted by several authors (plants: Nilsson & Svedmark, 2002; Baattrup-Pedersen et al., 2005; Wintle & Kirkpatrick, 2007; carabids: Bonn et al., 2002, Gerisch et al., 2006). River dynamics and flooding disturbance were considered as driving factors for the presence of riparian species and changing assemblage structures, as they lead to high spatiotemporal variability of transient habitat patches (compare Tabacchi et al., 1998 for plants and Van Looy et al., 2005 for carabids).

Although carabids responded less consistently to restoration than plants, the variability in their response was highest, with an increase of species number up to nine fold. The restored sections of ‘Gartroper Mühlenbach’ and ‘Rur Körrenzig’, where carabid species richness increased most strongly, were characterized by a complex assemblage of stress-tolerant, hygrophilous and eurytopic species. In contrast, assemblages of degraded, vegetated riparian zones without frequently inundated areas and the possibility of sediment relocation are mainly characterized by the presence of eurytopic plant and carabid species (Andersson et al., 2000; Baattrup-Pedersen et al., 2005; Lambeets et al., 2008a; Paetzold et al., 2008; Jähnig et al., 2009a).

There are, however, exceptions: while habitat richness increased in all 24 restored sections, the number of vegetation units decreased in one section, plant species richness decreased in two and carabid species richness in six restored sections. In case of decreasing plant species richness (e.g. river Nims) the non-restored sections offered ephemeral habitats for ruderal species, which were not present in the restored section. The cases with decreasing carabid beetles richness were characterized by exceptionally high richness of eurytopic species in the non-restored sections (in case of ‘Nidda Bad Vilbel’), by very low species richness in both

sections (in case of ‘Wurm’) or by already degenerated fixed embankments in non-restored sections, which allowed for some small gravel bars already colonized by stenotopic species (in case of Dill and Orke). Resulting diversity changes for carabid beetles were both positive and negative; the high abundance of individual stenotopic carabid beetles in some restored sections (e.g. *Bembidion decorum* at ‘Lahn Cölbe’ and *B. tibiiale* at ‘Bröl’) may decrease diversity, despite an increase in species numbers. This high variability reflects the sensitivity of carabids to changing microhabitat conditions (Rainio & Niemelä, 2003; Lambeets et al., 2009).

Mesohabitat number and diversity are most directly related to restoration measures: several mesohabitats were either created by these measures or generated shortly afterwards due to more frequent inundations. Local river-related processes, especially inter-annual variation in flood disturbance and dispersal along the river corridor, mainly determine patterns of riparian plant richness (Renöfält et al., 2005). The redistribution of organic and inorganic matter in restored sections offers habitats, required for the colonization and establishment of (hydrochorous dispersed) propagules (Gurnell et al., 2007; Riis, 2008).

3.4.2 Restoration effects on taxonomic diversity

Overall, taxonomic diversity of plant species was not significantly affected by restoration, taxonomic diversity of carabid beetles decreased. On the level of individual rivers, taxonomic plant diversity increased in two thirds of the cases, while it decreased more often in case of carabid beetles. The main riparian habitat types generated by the restoration measures were sparsely vegetated gravel and sand bars. Plant species specialized on these habitats belong to a wide variety of families and genera, while other species of these groups are typical representatives of more stable habitats characteristic for non-restored sections. Consequently, there was not much difference between plant taxonomic diversity of restored and non-restored sites, unless species number was greatly increased. In contrast, most carabid species, which are bound to sand and gravel bars, belong to the genus *Bembidion* (Manderbach & Hering, 2001) as most of *Bembidiini* ssp. were adapted to live in riverine sediments due to their small and flattened body, and to flood disturbances due to well-developed wings and flight-muscles (Desender & Turin, 1989). Dependent on properties of the substratum, moisture conditions (Andersen, 1978) and vegetation density (Van Looy et al., 2005), they prefer specific habitats on the river bank (Andersen, 1970). Therefore, the resulting communities in restored sections were taxonomically more homogeneous, although they bear a wider range of ecological traits. In contrast, non-restored sections were inhabited by a mixture of different genera, including

eurytopic species, e.g. *Pterostichus melanarius* or *Loricera pilicornis* similar to the findings of Van Looy et al. (2005) who found them in less dynamic riparian areas.

3.4.3 Restoration effects on assemblage functional indices

Assemblage functional indices of restored river sections were positively affected by morphological changes but not by the time since restoration. Initiated by restoration, flood dynamics affected spatiotemporal mesohabitat heterogeneity by building up transient habitat patches over and over again (Rohde et al., 2005). This leads to a mosaic of differing habitat patches from sparsely vegetated banks at the shoreline to vegetated embankments, resulting in increased plant diversity and complex assemblages with stenotopic and eurytopic species. Restored sections were inhabited by typical stress-tolerant pioneers of plant species such as *Veronica beccabunga*, *Nasturtium officinale* and *Calamagrostis epigejos*, which are adapted to the high turnover of riparian habitats and indicating fluctuating water levels. Increased number and cover of riparian plant species were effects of restoration measures following habitat changes (compare Baattrup-Pedersen et al., 2000). The time since restoration did not limit the colonization of pioneer vegetation (Rohde et al., 2005), if flow dynamics constantly recreate bare riparian banks.

As carabid assemblages are mainly determined by flooding disturbance, vegetation density and the presence of silt (Van Looy et al., 2005), they strongly benefit from dynamic habitat turnover and resulting multiple vegetation patterns. Carabid species such as *Bembidion atrocaeruleum*, *B. femoratum* and *B. punctulatum* were restricted to restored sections due to their strong association with sand and gravel banks (Eyre et al., 2001; Günther & Assmann, 2005). High abundances of *Bembidion* ssp. were also observed by Van Looy et al. (2005) and Lambeets et al. (2008a), widely dispersed along the Common Meuse river banks (Belgium).

Although the abundance and number of stress-tolerant pioneers of carabids changed less frequently than for plants, the magnitude of change was even greater. The frequency of positive effects for plants may be due to the higher species pool in the catchments. Plants show various passive dispersal mechanisms e.g. hydrochory (Burkart, 2001) or anemo-/zoochorous seed dispersal (Johansson & Nilsson, 1996; Soons, 2006). In contrast, carabid beetles colonize both by passive dispersal and active flight (Bates et al., 2006), leading to higher dispersal ability. Main factors for a successful dispersal of riparian species and their colonization of new habitats are flooding disturbance, which increases the rate of dispersal, and a natural distribution of appropriate habitat patches (Bates et al., 2006). The differences in response of stress-tolerant carabid pioneers may result from the different frequency of suited habitats in the catchments; if remnant populations of riparian carabids still occur, however, they can colonize

newly generated habitats rapidly and intensively, as most of them are full-winged spring breeders (Den Boer, 1970, 1990b). Flight muscle development as a coadapted trait, required for seasonal migration between habitats for reproduction and for hibernation, leads to high dispersal ability (Desender, 2000).

Hygrophilous species including also species that were not necessarily bound to riparian areas (e.g. *Carabus granulatus*, *Limodromus assimilis*) did not benefit from restoration, rejecting our hypothesis. The abundance of hygrophilous plant and carabid species was highly variable and not generally due to increased floodplain areas. Microhabitat differences of river sections in terms of the presence or absence of silt, additionally affecting the occurrence of hygrophilous species (Lambeets et al., 2008b), may be an explaining variable.

3.5 Conclusion

Based on 24 study sites we conclude that restoring river hydromorphology has almost generally positive effects on riparian habitats and riparian biodiversity, confirming the results of single reach studies. This observation strongly differs from experiences made with aquatic organism groups, which are often weakly or not at all affected by the restoration of river habitats. Future management of river banks should still focus on creating morphological heterogeneity and initiating dynamic processes as riparian organism groups benefit strongly from habitat improvements. Moreover, remaining patches of natural habitats with source populations or residual species should be considered in the planning process of restoration measures as it might accelerate successful colonization of restored river sections.

Riparian plants and carabids are suitable bioindicators for restoration success as they react strongly to morphological improvements of the river floodplain. Indices, e.g., richness of riparian plant and carabid species, especially stress-tolerant species which are well adapted to dynamic riparian areas should be considered in the assessment of restoration success.

4 Habitats and species assemblages in the Ruhr river and floodplain: timescales in restoration effects

4.1 Introduction

River restoration has multiple effects of habitats, biota and processes, but effect sizes and time spans required for response differ between parameters.

Organism groups inhabiting the rivers and their floodplains depend on habitat composition and are thus supposed to benefit from structural enhancement. However, benthic invertebrates and fish rarely respond to morphological restoration, as multiple stressors affect the assemblages or restoration improved aquatic habitats (Miller & Kochel, 2010; Jähnig et al., 2010). Furthermore, recolonization might be limited by an impoverished species pool in the surroundings of restored sections (Sundermann et al., 2011a; Stoll et al., 2013) or longitudinal disruptions of the river network (Bunn & Arthington, 2002). In contrast to benthic invertebrates and fish, aquatic macrophytes, though less investigated (Feld et al., 2011), respond more positive to improved habitat conditions (Henry et al., 2002; Pedersen et al., 2007; Lorenz et al., 2012). Riparian organism groups respond strongly to morphological changes, especially carabid beetles (Günther & Assmann, 2005; Lambeets et al., 2008a; Zulka, 2008). While there are some studies addressing several organism groups simultaneously (Stranko et al., 2012; Haase et al., 2013; Lorenz & Feld, 2013; Bonn et al., 2002; Follner & Henle 2006; Lambeets et al., 2008a), there is no study comparing the effects on benthic invertebrates, fishes, aquatic macrophytes, riparian vegetation and riparian beetles.

The temporal development of assemblages after restoration is poorly understood, although longer time spans for successful colonization of restored sections by aquatic organism groups are suggested (Lorenz et al., 2009; Bernhardt & Palmer, 2011). Monitoring studies spanning more than one or two years are scarce and restoration measures with an age of more than 10 years have rarely been addressed (Feld et al., 2011). It can be expected that assemblages differ in their succession, but usually start with an initial phase of pioneer colonization following the creation of new habitats in the river and its floodplain. A comprehensive investigation of the succession of aquatic and riparian habitats and species following restoration is still missing.

We investigated habitat compositions in the aquatic and riparian zone and 5 organism groups (benthic invertebrates, fish, aquatic macrophytes, carabid beetles, floodplain vegetation) in 6 sample sections of the mountain river Ruhr in Germany.

We compared habitats and species assemblages between young restored sections, which were stepwise restored from 2007 to 2009, non-restored sections (upstream and downstream of the restored reach) and an old restored section with a passive development since 1990 downstream of all other sections. Investigations started in 2008, the year after the first section was restored, and continued 3 to 5 years.

The aim of this chapter is to compare restoration effects between different time spans after restoration and between aquatic and riparian habitats and organism groups. We expected:

- Aquatic and riparian species assemblages are determined by habitat homogeneity of non-restored sections and by habitat heterogeneity of restored sections.
- Changes in species assemblages depend on the timescale: species colonizing newly created aquatic and riparian habitats in recently restored sections have high dispersal abilities, e.g., riparian carabid beetles. The old restored section is additionally inhabited by competitive species with low dispersal ability.
- The magnitude of restoration effects differs between organism groups: aquatic organism groups respond slower and weaker to restoration than riparian organism groups.

4.2 Sample sections and field work

4.2.1 Sample sections

We investigated 6 sample sections of the Ruhr near Arnsberg-Neheim (North Rhine-Westphalia, Germany; Figure 4-1a, b): one non-restored section upstream (N1), three sections restored between 2007 and 2009 (Y1-Y3), a non-restored section downstream (N2) and an old restored section (O1) passively developing since 1990 (Table 4-1). Non-restored sections reflect the condition of river sections prior to restoration and are characterized by a straightened channel form and fixed embankments (Figure 4-2).

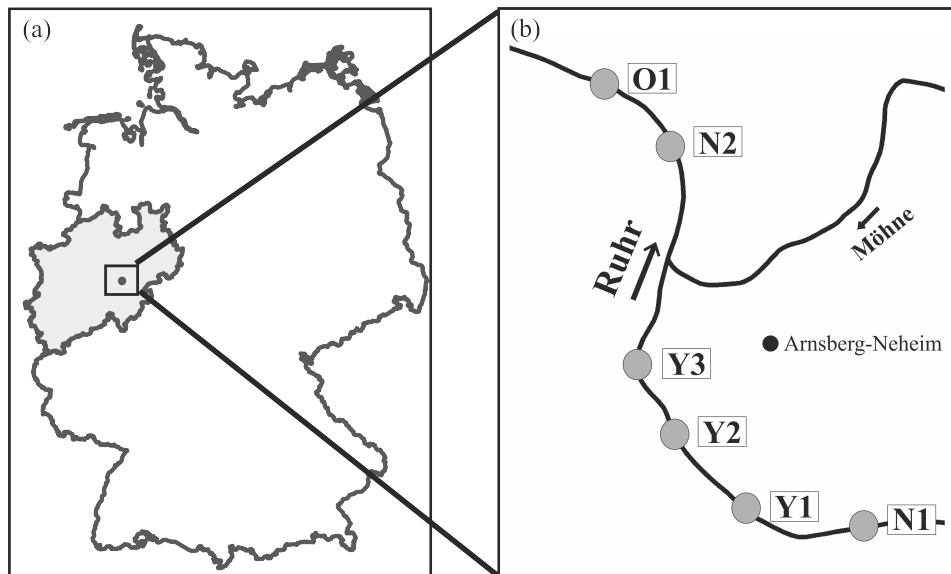


Figure 4-1: Location of the study area in the Federal State of North Rhine-Westphalia (a) and position of the sample sections of the river Ruhr near Arnsberg-Neheim (b); N1 = non-restored section upstream, Y1-Y3 = young restored sections; N2 = non-restored section downstream; O1 = old restored section.

Restoration measures upstream from the Möhne mouth (Y1-Y3) were stepwise implemented from 2007 to 2009 on a river length of 2.7 km, in the following named ‘young restored sections’ (Figure 4-3). Measures aimed at creating morphological heterogeneity, reconnection of floodplain areas and the improvement of flooding prevention. All measures comprised the removal of fixed embankments and the addition of deadwood. Moreover, the entrenchment depth was lowered by regrading slopes and adding coarse gravel to the river bottom and the riparian areas. In the section Y1 which was restored at the end of 2007, measures were mainly implemented at the right bank including the creation of small secondary channels. Additionally, a gravel depot was placed in the upper part of the restored section in 2010. In the sections Y2 and Y3, the river channel was widened. Parts of the former wooded embankments on the left side were retained as islands in the middle of the new river channel.



Figure 4-2: Non-restored section N2 against flow direction (June 2010).

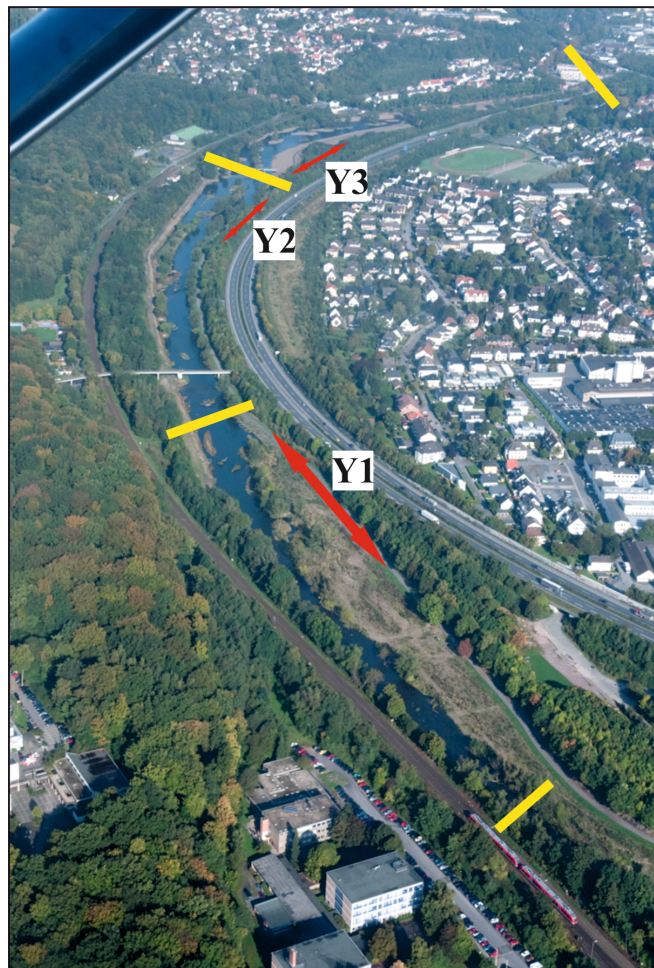


Figure 4-3: Young restored sections Y1-Y3 of the river Ruhr in flow direction (modified after NZO GmbH, September 2009); yellow bars = borders of the restored sections; red arrows illustrate the sample sections.

Table 4-1: Sample sections in the Ruhr river and floodplain, abbreviations, geographic positions, length of restored sections and year of restoration. Sample sections were ordered from up- to downstream.

Abbreviation of sample section	N1	Y1	Y2	Y3	N2	O1
Status of sample section	Non-restored section upstream	Young restored section	Young restored section	Young restored section	Non-restored section downstream	Old restored section
Latitude [decimal, WGS84]	7.97850	7.96272	7.95380	7.95159	7.95359	7.94777
Longitude [decimal, WGS84]	51.43974	51.44104	51.44738	51.44979	51.46594	51.46872
Year of restoration	-	2007	2008	2009	-	~1990
Length of restored section [m]	-	750	820	960	-	320

The old restored sections O1 (Figure 4-4) underwent a passive development since ~20 years. In 1980, the highway north from the river was aligned and, therefore, the river bed was shifted to southwest. From 1990 on, decaying bank fixations were not repaired on the left side of the river. Following lateral bank erosion a secondary channel and a huge island between the main and the secondary channel developed. On the left side of the secondary channel, an eroding cliff appeared and is still eroding every winter due to high discharges.



Figure 4-4: Old restored section O1 in the river Ruhr (Hammerschmidt, Stadt Arnsberg; April 2011). The river is fixed on the north bank by the highway but erodes the southern bank.

Between the sample sections N1, Y1-3 and the sections N2, O1 the river type changes according to the German stream typology from a mid-sized ($> 100\text{-}1,000\text{ km}^2$ catchment area) to a large ($> 1,000\text{-}10,000\text{ km}^2$ catchment area) river due to the confluence with the Möhne river.

4.2.2 Field work

Sampling was done on a length of 200 m per sample section. Investigations started in 2008 and were continued till 2012 once a year. The number of sample years differed between sample sections and organism groups (Figure 4-5). We surveyed aquatic and riparian meso- and microhabitats in June and July at low flow conditions along ten transects per river section with an equal distance of 20 m spanning the area between the top edges of the embankment. We recorded mesohabitats based on Raven et al. (1997) and Jähnig et al. (2008) and measured their lengths along the transects to determine the proportion of habitats per river section. Within the riparian channel features, we also recorded the microhabitats. Aquatic microhabitats were recorded at 10 points per transects, equally distributed within the aquatic channel features. Table 4-2 and Table 4-3 give an overview of recorded meso- and microhabitats. Detailed information morphological sampling is given in chapter 2.1.

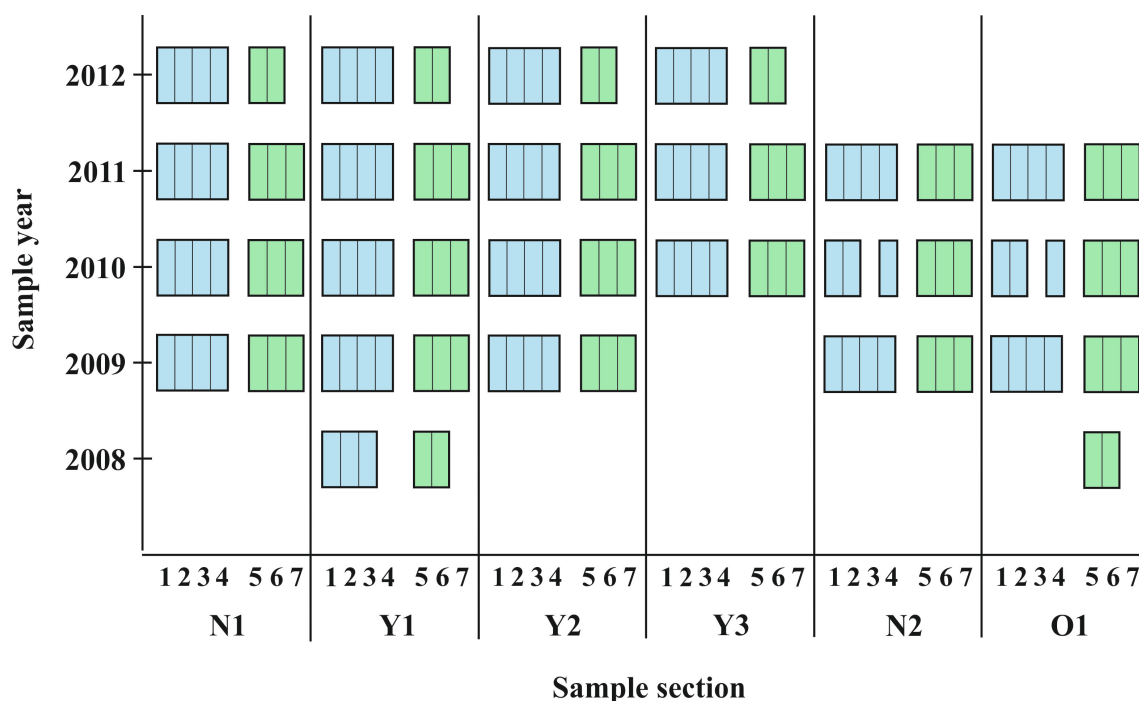


Figure 4-5: Time table of sampling in the Ruhr river sections. Aquatic area (□): 1 = aquatic habitats, 2 = benthic invertebrates, 3 = fish, 4 = aquatic macrophytes; riparian area (■): 5 = riparian habitats, 6 = carabid beetles and 7 = floodplain vegetation.

Table 4-2: Recorded mesohabitats and abbreviations used in analyses.

	Mesohabitat	Abbreviation
Aquatic zone	Main channel	mainc
	Secondary channel	secc
	Connected sidearm	cons
	Disconnected sidearm	discs
	Permanent standing water body	psw
	Temporary standing water body	tsw
Riparian zone	Bank with woody vegetation	wbank
	Bank with herbaceous vegetation	hbank
	Side bar/midchannel bar	bar
	Island with woody vegetation	wisl
	Island with herbaceous vegetation	hisl
	Artificial embankment	aemb
	Embankment with woody vegetation	wemb
	Embankment with herbaceous vegetation	hemb
	Eroding cliff	ecl
	Floodplain area	flood

Table 4-3: Recorded microhabitats and abbreviations used in analyses.

	Microhabitat	Abbreviation
Aquatic and riparian zone	Macrolithal/Technolithal	tech
	Mesolithal	meso
	Microlithal	micro
	Akal	akal
	Psammal	psam
	Argyllal	arg
	Xylal	wood
	CPOM	cpom
	FPOM	fpom
Aquatic zone only	Algae	alg
	Submerse macrophytes	smac
	LPTP	ltp

Benthic invertebrates were sampled using a multihabitat-sampling design (Meier et al., 2006), fish were investigated by electrofishing according to Diekmann et al. (2005) and aquatic macrophytes were surveyed by using the German standard method (Schaumburg et al., 2004, compare also Lorenz et al., 2012). For floodplain vegetation and carabid beetles, a grab-sampling method was used. Detailed information about the sampling methods of organism groups and the preparation of taxalists are given in chapter 2.2.

4.3 Data processing and analyses

4.3.1 Restoration effects on aquatic and riparian habitats and species assemblages

We calculated a Bray-Curtis distance matrix using arcsine squareroot transformed meso- and microhabitat data and log-transformed taxalists. Based on these distance matrices, we performed non-metric multidimensional scaling (NMS) with the software Primer 6. We chose descriptive methods as statistical group analyses and significance tests, e.g., ANOSIM or MRPP, were not appropriate because the number of samples per group differed strongly (e.g., for fish between two samples in the old restored section and 12 samples in young restored sections). We evaluated variations in habitat and species compositions due to the status of sample sections (non-restored, young restored, old restored) and differences between sample sections by displaying post-hoc defined sample groups in the NMS plots. In the NMS plots of meso- and microhabitat data, we additionally displayed underlying habitats as vectors which showed a Pearson correlation > 0.2 between habitats and the ordination axis.

4.3.2 Species indicating the status of sample sections

We used indicator species analysis to identify species particularly inhabiting non-restored, young restored or old restored sections. Analyses were based on log-transformed abundance data. We used the software R (Ihaka & Gentleman, 1996) and the package ‘indicspec’ (De Cáceres et al., 2010) to perform ‘multi-level pattern’ analysis. This analysis addresses the relationship between species patterns and combinations of groups of sections and corrects for unequal sample sizes amongst groups based on abundance data. It allows a comparison of sample groups with differing number of samples and identifies species which indicate two conditions simultaneously, e.g., young and old restored sections. The strength of the association between species and the sample groups is given by the indicator value (IndVal value) ranging from 0 (no association) to 1 (maximum association); statistical significance was given after permutation procedures.

4.3.3 Magnitude of restoration effects on aquatic and riparian habitats and species assemblages

We calculated mean dissimilarities between non-restored, young and old restored sections using the software R and the package ‘vegan’ (Oksanen et al., 2013) to analyze the magnitude of restoration effects on habitat types and organism groups. On the basis of pairwise comparison of mean dissimilarities between non-restored, young and old restored sections, we evaluated potential differences of habitat and species composition between young and old restored sections.

4.4 Results

4.4.1 Restoration effects on the aquatic zone

4.4.1.1 Aquatic micro- and mesohabitats

Samples of aquatic mesohabitats split up in three groups (Figure 4-6a) reflecting effects of restoration. Young and old restored sections differed from non-restored sections due to the occurrence of additional mesohabitats, e.g., connected sidearms ('cons') and standing water bodies ('psw' and 'tsw'). The restored sections Y2 and Y3 and the old restored section O1 featured with 23% to 48% a high proportion of secondary channels ('secc') and permanent standing water bodies ('psw') which were only present in these sample sections. The young restored section Y1 differed from the other restored sections in a higher proportion of the main channel ('mainc') with 78% to 90%, a low proportion of secondary channels ('secc') with less than 7% and the presence of sidearms ('disc' and 'conc') and temporary standing water bodies ('tsw').

For aquatic microhabitats, we detected differences between non-restored and restored sections (Figure 4-6b). Non-restored sections were mainly characterized by artificial substrates ('tech'), i.e. riprap. In contrast, restored sections featured a diverse array of finer mineral and organic substrates of variable proportions, e.g. fine to medium-sized gravel ('akal') or fine particular organic matter ('fpom'); furthermore deadwood ('xylal') and submerged macrophytes ('smac') were present. Due to the presence of artificial substrates (7% to 17%) and the dominance of fist to hand-sized cobbles ('meso'), the old restored section O1 and the young restored section Y1 showed higher similarity to non-restored sections than the other restored sections.

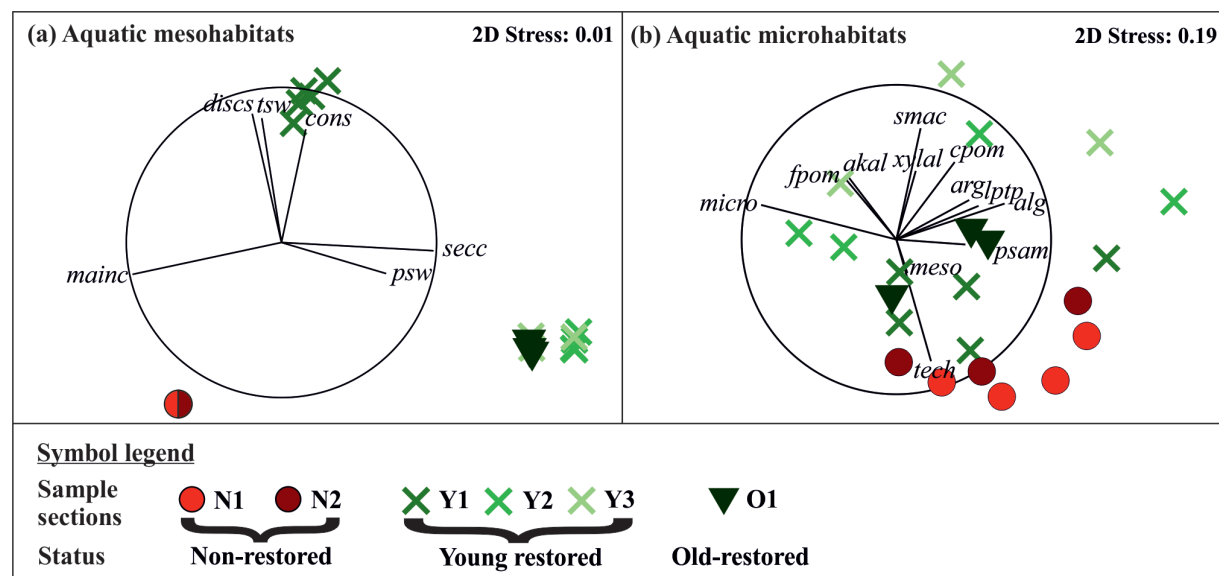


Figure 4-6: Two-dimensional distribution of samples in NMS-ordinations based on arcsine squareroot transformed aquatic habitat data using Bray Curtis similarity: aquatic mesohabitats (a) and aquatic microhabitats (b). Plotted habitat vectors define Pearson correlation (> 0.2) between habitats and the ordination axis.

4.4.1.2 Aquatic organism groups

Assemblage compositions of aquatic macrophytes showed obvious differences between non-restored, young restored sections and the old restored section. However, benthic invertebrates (Figure 4-7a) and fish did not respond to restoration.

Fish samples tended to split up between sections up- and downstream from the Möhne tributary (Figure 4-7b), especially the non-restored section N2 differed strongly from all other sections. Upstream of the Möhne mouth, all sections were colonized by species typical for the grayling zone such as bullheads (*Cottus gobio*), minnows (*Phoxinus phoxinus*), chubs (*Leuciscus cephalus*) and stone loaches (*Barbatula barbatula*). All species showed high abundances of young-of-the-year fishes in these sections. Downstream from the Möhne mouth, both the non-restored (N2) and the old restored (O1) section were inhabited by nearly the same species as upstream, but abundances of all species were obviously lower for adult and young-of-the-year fishes.

Assemblages of aquatic macrophytes clearly separated between non-restored, young restored and the old restored section (Figure 4-7c). Non-restored sections were species-poor (4 ± 1.2 species) and mainly colonized by *Fontinalis antipyretica* and *Cladophora* sp. In contrast, we found higher species richness (12 ± 2.4 species) in the restored sections. The old restored section differed from the young restored sections in higher abundances of *Fontinalis antipyretica*, while parvopotamids (*Potamogeton* ssp.) and helodids were rare.

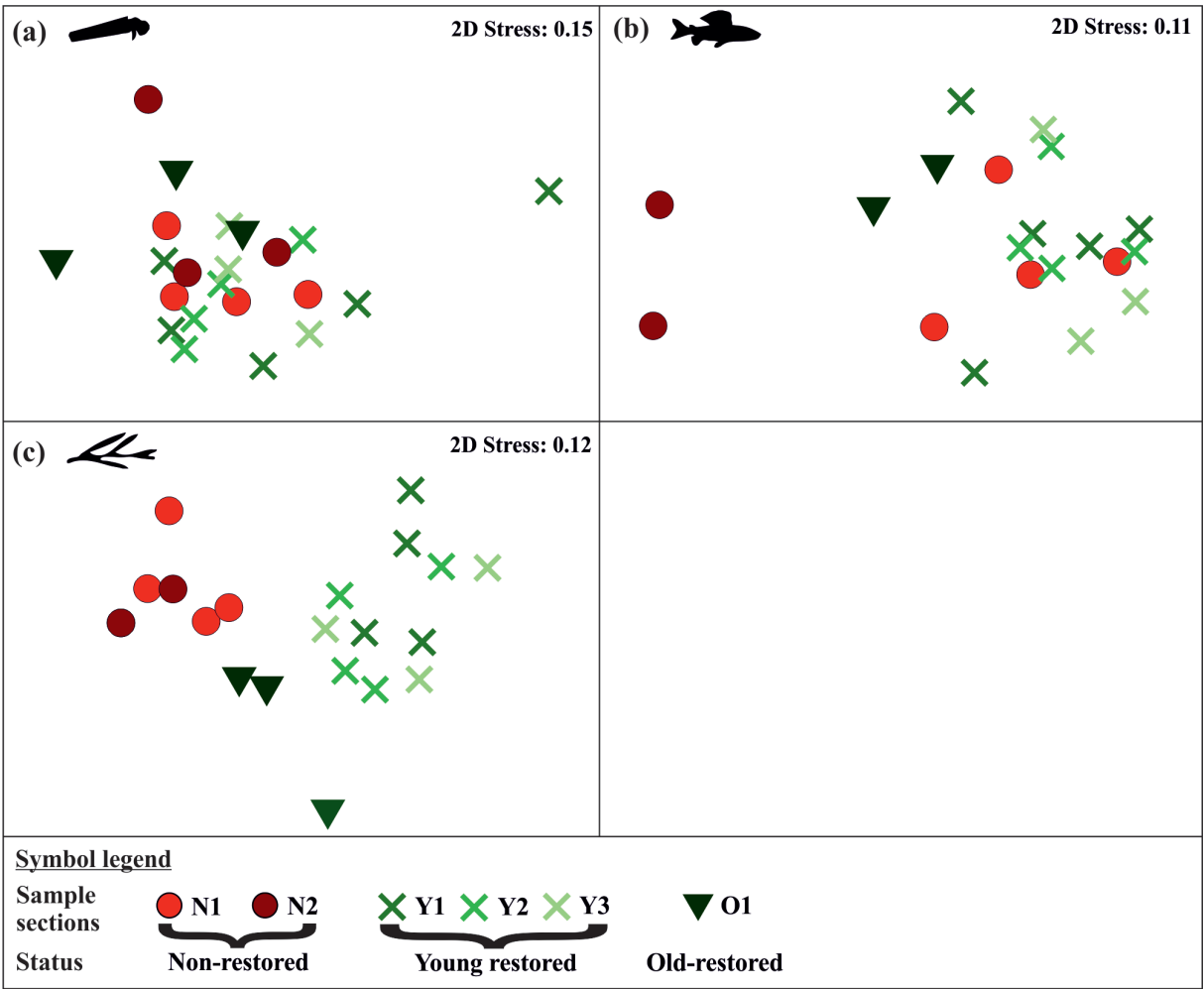


Figure 4-7: Two-dimensional distribution of samples in NMS-ordinations based on log-transformed abundance data of aquatic organism groups using Bray Curtis similarity: benthic invertebrates (a), fish (b), aquatic macrophytes (c).

4.4.2 Restoration effects on the riparian zone

4.4.2.1 Riparian micro- and mesohabitats

Riparian mesohabitats clearly separated between non-restored, young restored sections and the old restored section (Figure 4-8a). The young restored section Y1 was mainly composed of a huge floodplain area (‘floodp’), woody islands (‘woodisl’) and eroding cliffs (‘ecl’), whereas the young restored section Y2 and the old restored section O1 were each characterized by a huge island with herbaceous vegetation (‘herbisl’) between the main and the secondary channel. All young restored sections were characterized by the presence of bars (‘bar’) with highest proportions in the youngest restored section Y3 and lowest in the old restored sections.

Riparian microhabitat compositions also clearly differed between the non-restored and the young sections and the old restored section (Figure 4-8b). Riparian areas in non-restored sec-

tions were strongly dominated by silt, loam and clay ('arg') and artificial substrates ('techno'), e.g. riprap, with slightly higher proportions of fist to hand-sized cobbles ('meso') and sand ('psam') in the non-restored section N2. In contrast, restored sections were mainly composed of fist to hand-sized cobbles ('meso') and coarse gravel ('micro') with variable portions of finer mineral, e.g. fine gravel ('akal') and organic substrates, e.g. fine particulate organic matter ('fpom'). Samples of the old restored sections mainly ranked between non-restored and young restored sections.

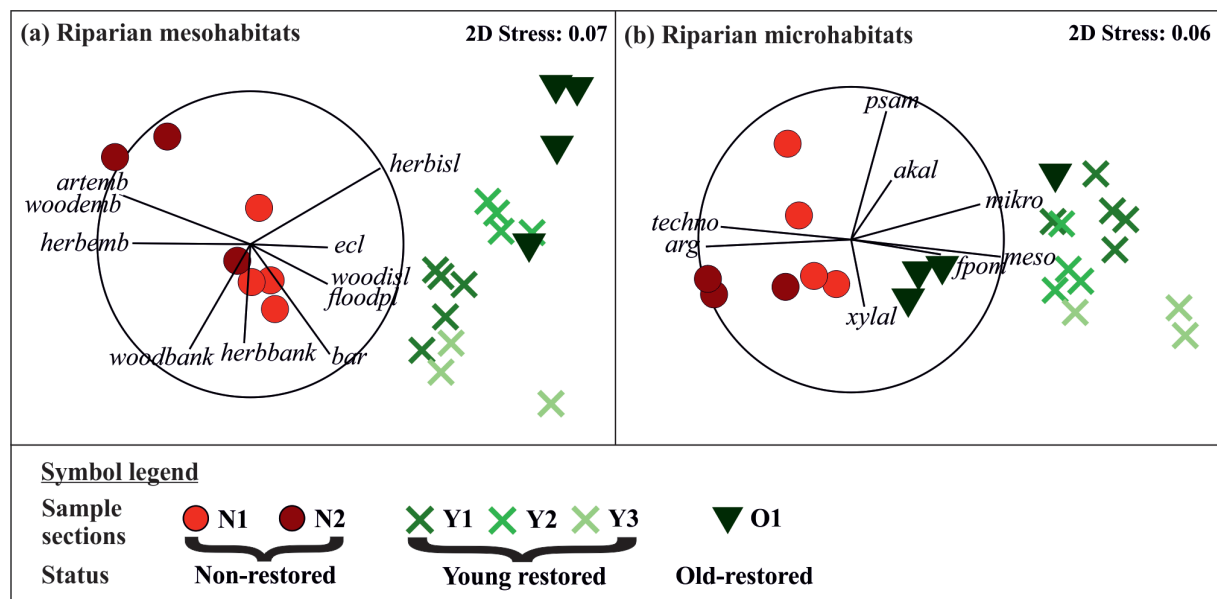


Figure 4-8: Two-dimensional distribution of samples in NMS-ordinations based on arcsine squareroot transformed riparian habitat data using Bray Curtis similarity: riparian mesohabitats (a) and riparian microhabitats (b). Plotted habitat vectors define Pearson correlation (> 0.2) between habitats and the ordination axis.

4.4.2.2 Riparian organism groups

Compositions of carabid beetle assemblages strongly differed between the non-restored, young-restored sections and the old restored section (Figure 4-9a). In non-restored sections, we found 7 to 12 species with a high dominance of eurytopic species, e.g., *Bembidion tetracolum* and species preferring vegetated habitats, e.g., *Limodromus assimilis*. Restored sections showed on average nearly doubled species richness than non-restored sections (15.7 ± 2.7 species compared to 8.8 ± 1.7). Young restored sections were characterized by a high number and high abundances of species with a preference for bars, e.g. *Bembidion decorum*, *B. atrocaeruleum* and *B. punctulatum*. In addition to riparian specialists found in young restored sections, the old restored section was colonized by further riparian specialists, e.g., *Bembidion*

millerianum, and species with several habitat preferences such as species preferring vegetated banks, e.g., *Bembidion dentellum*, species typical for forests, e.g. *Pterostichus cristatus* or species typical for cultivated landscape, e.g. *Harpalus rufipes*.

Similar to carabid beetles, samples of floodplain vegetation clearly separated between non-restored, young restored and the old restored section (Figure 4-9b). Non-restored sections were mainly colonized by competitive and widely distributed species, e.g., *Fraxinus excelsior* and *Urtica dioica*. Species richness in young restored sections was higher than in non-restored sections (45.0 ± 10.5 species compared to 30.8 ± 4.6). Young restored sections showed high abundances of commonly distributed grassland and pioneer species, e.g., *Trifolium* ssp.; species bound to transient and moist areas, e.g., *Lythrum salicaria*, were just sporadically present. In contrast, the old restored section was colonized by species preferring moist areas, e.g., *Rorippa* ssp., but also by ruderal and competitive species with high light preference, e.g., *Barbarea vulgaris* and *Tanacetum vulgare*. Species richness in the old restored section was similar to young restored sections.

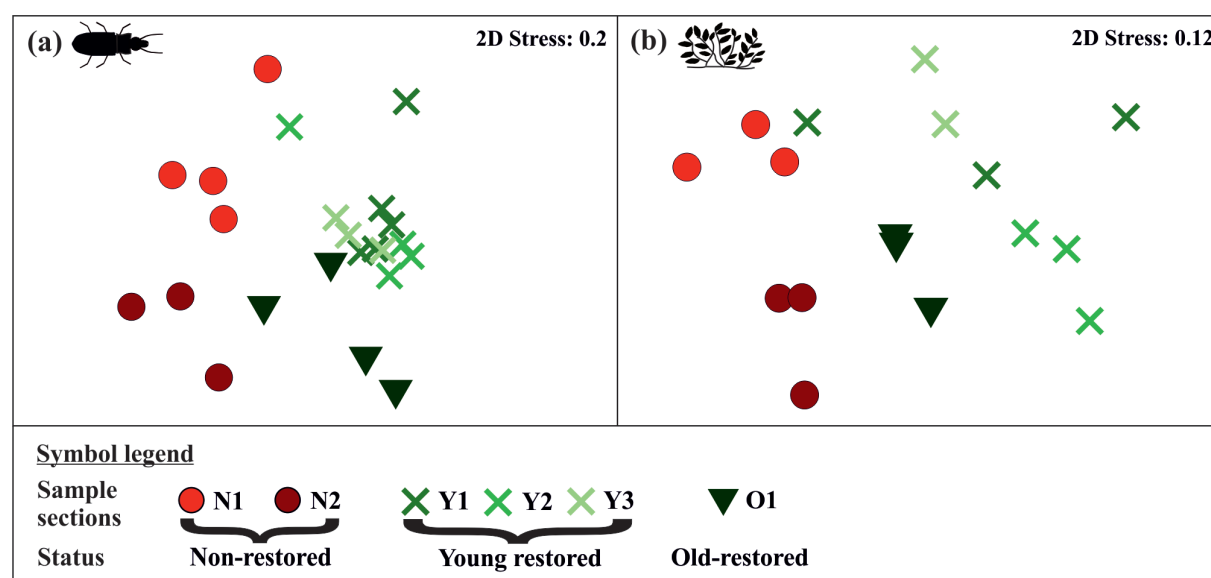


Figure 4-9: Two-dimensional distribution of samples in NMS-ordinations based on log-transformed abundance data of riparian organism groups using Bray Curtis similarity: carabid beetles (a) and floodplain vegetation (b).

4.4.3 Species indicating the status of sample sections

We found ten aquatic species indicating differences in the status of sample sections (Table 4-4). Aquatic macrophytes comprised seven indicator species (20.6% of all macrophyte species); four of which (*Phalaris arundinacea*, *Callitriche* sp., *Elodea nuttallii*, *Veronica beccabunga*) were found in restored sections in general. For benthic invertebrates and fish we did

not find indicator species for young restored sections but e.g., *Gammarus pulex* and *Anguilla anguilla* were specific for non-restored sections and the old restored sections and *Perca fluviatilis* for the old restored section.

Table 4-4: Benthic invertebrate, fish and aquatic macrophyte species indicating the status of sample sections; * = significant for $p < 0.05$; ** = highly significant for $p < 0.01$; n = total number of species in all samples; in case of fish the total number of species including young-of-the-year as pseudospecies.

Organism group	Non-restored sections	Young restored sections	Old restored section	Speciesname	IndVal value
Benthic invertebrates (n = 102)				<i>Gammarus pulex</i>	0.827*
Fish (n = 29)				<i>Perca fluviatilis</i>	0.625*
				<i>Anguilla anguilla</i>	0.843*
Aquatic macrophytes (n = 34)				<i>Iris pseudacorus</i>	0.764*
				<i>Rorippa amphibia</i>	0.816*
				<i>Phalaris arundinacea</i>	0.948**
				<i>Callitriche</i> sp.	0.931**
				<i>Elodea nuttallii</i>	0.931**
				<i>Veronica beccabunga</i>	0.894**
				<i>Fontinalis antipyretica</i>	0.914**

Riparian organism groups (Table 4-5) comprised a comparatively high number of indicator species (11 species = 18.6% of all carabid and 21 species = 16.5% of all plant species). Four of the carabid indicator species particularly inhabited the old restored sections. Five carabid species, almost exclusively belonging to the genus *Bembidion*, were indicators for the young restored sections and the old restored section. Floodplain vegetation supported six species (4.7% of all plant species) exclusively specific for young restored sections (e.g., *Ranunculus repens*, *Trifolium dubium*) and eight species (6.3 % of all plant species) exclusively specific for the old restored section (e.g., *Barbarea vulgaris*, *Vicia sepium*). Four plant species were typical for the young restored sections and the old restored section.

Table 4-5: Carabid beetle and floodplain vegetation species indicating the status of sample sections; * = significant for $p < 0.05$; ** = highly significant for $p < 0.01$; n = total number of species in all samples.

Organism group	Non-restored sections	Young restored sections	Old restored section	Speciesname	IndVal value
Carabid beetles (n = 59)				<i>Bembidion millerianum</i>	0.879**
				<i>Harpalus rufipes</i>	0.707*
				<i>Pterostichus cristatus</i>	0.707*
				<i>Bembidion dentellum</i>	0.604*
				<i>Bembidion atrocaeruleum</i>	0.979**
				<i>Bembidion decorum</i>	0.960**
				<i>Bembidion punctulatum</i>	0.901**
				<i>Elaphrus riparius</i>	0.791*
				<i>Bembidion articulatum</i>	0.750*
				<i>Pterostichus strenuus</i>	0.713*
				<i>Bembidion schueppelii</i>	0.704*
Floodplain vegetation (n = 128)				<i>Crataegus monogyna</i>	0.816*
				<i>Ranunculus repens</i>	1.000**
				<i>Trifolium dubium</i>	0.935**
				<i>Trifolium repens</i>	0.870**
				<i>Lotus corniculatus</i>	0.866**
				<i>Trifolium pratense</i>	0.866**
				<i>Epilobium montanum</i>	0.707*
				<i>Barbarea vulgaris</i>	1.000**
				<i>Vicia sepium</i>	0.946**
				<i>Tanacetum vulgare</i>	0.917**
				<i>Rorippa sylvestris</i>	0.882**
				<i>Rorippa palustris</i>	0.862**
				<i>Galium mollugo</i>	0.851**
				<i>Chenopodium polyspermum</i>	0.816*
				<i>Bromus sterilis</i>	0.751*
				<i>Artemisia vulgaris</i>	0.921*
				<i>Plantago lanceolata</i>	0.891**
				<i>Poa pratensis</i>	0.822*
				<i>Scrophularia nodosa</i>	0.798*
				<i>Calystegia sepium</i>	0.953*
				<i>Lamium maculatum</i>	0.834*

4.4.4 Magnitude of restoration effects on aquatic and riparian habitats and species assemblages

Restoration influenced habitat compositions both in the aquatic and the riparian area with different magnitude. Using mean dissimilarities between the sample groups of non-restored, young restored and the old restored section (Table 4-6), we detected highest effects on riparian mesohabitats (46.8%), followed by riparian microhabitats (39.8%), aquatic mesohabitats (32.4%) and aquatic microhabitats (27.1%).

We found highest differences between non-restored and young restored sections for riparian microhabitats with a mean dissimilarity of 55.2 %. For riparian mesohabitats, we detected the overall highest dissimilarity of habitat compositions with 61.4 % between non-restored and old-restored sections.

Table 4-6: Mean dissimilarities [%] between non-restored, young and old restored sections and pair-wise calculated mean dissimilarities for aquatic and riparian habitats; highest value per habitat type in bold letters.

	Mean dissimilarity between groups	Non-restored vs. young restored sections	Non-restored sections vs. old restored section	Young restored sections vs. old restored section
Aquatic mesohabitats	32.4	39.5	37.0	20.8
Aquatic microhabitats	27.1	30.8	25.4	25.0
Riparian mesohabitats	46.8	41.8	61.4	37.2
Riparian microhabitats	39.8	55.2	34.3	30.1

Organism groups differed strongly in their reactions to restoration (Table 4-7). We detected obvious restoration effects on aquatic macrophytes, carabid beetles and floodplain vegetation. Non-restored, young sections and the old restored section clearly separated with mean dissimilarities between the sample groups of 67.1% for carabid beetles, 56.4% for aquatic macrophytes and 55.6% for floodplain vegetation. For each of the three organism groups, assemblages of non-restored and young restored sections differed strongest. In contrast, assemblages of benthic invertebrates and fish did not show clear restoration as dissimilarities between sample groups were low (35% to 38% for benthic invertebrates and 21% to 24% for fish).

Table 4-7: Mean dissimilarities [%] between non-restored, young and old restored sections and pair-wise calculated mean dissimilarities for benthic invertebrates, fish, aquatic macrophytes, carabid beetles and floodplain vegetation; highest value per organism group in bold letters.

	Mean dissimilarity between groups	Non-restored vs. young restored sections	Non-restored sections vs. old restored section	Young restored sections vs. old restored section
Benthic invertebrates	36.0	35.1	35.4	38.6
Fish	23.4	24.0	23.8	21.3
Aquatic macrophytes	56.4	60.0	52.8	51.1
Carabid beetles	67.1	71.4	70	57.6
Floodplain vegetation	55.6	59.1	51.5	51.6

4.5 Discussion

4.5.1 Restoration effects on the aquatic zone and potential of indicator species

Slight changes in habitat compositions of the aquatic zone due to restoration were obvious. Differences in macrophyte assemblages between the young restored sections and the old restored section mainly resulted from differences in habitats and not from the timescale. Benthic invertebrates and fish assemblage compositions were not driven by restoration neither in the young-restored nor in the old restored section.

Restoration increased habitat diversity by establishing aquatic mesohabitats, e.g., secondary channels and standing water bodies which are typical for natural sections of mountain rivers. The river bottoms of all sample sections were mainly composed of fist to hand-sized cobbles resulting in overall low dissimilarities between sample sections. However, restoration increased microhabitat diversity on the river bottom, especially in case of the young restored sections Y2 and Y3. In areas with low current, e.g. secondary channels, and upstream from placed deadwood, finer organic and mineral sediments deposited.

Aquatic macrophytes responded strongly to restoration; the improved meso- and microhabitat diversity increased macrophyte richness and abundance. Restored sections were colonized by various species belonging to different growth forms. The classification of growth forms (compare Appendix 6d) groups macrophyte species according to their form and structure of leaves and roots (Den Hartog & Van der Velde, 1988) and reflects, therefore, differing adaptations to environmental conditions. Similar to the results of Lorenz et al. (2012), Elodids, Helodids, Parvopotamids and Peplids were almost exclusively present in restored sections. Thereby, Helodids supported the highest number of species (13) benefitting from the shallow and frequently flooded banks in riparian areas. The importance of these areas was also high-

lighted by Pedersen et al. (2007). Significantly higher abundances in both, the young restored sections and the old restored section, compared to non-restored sections showed *Phalaris arundinacea* preferring nutrient rich, moist riparian areas, *Callitriche* sp. typical for nutrient rich aquatic areas with low or no current, *Elodea nuttallii* colonizing areas with low current and water depth and *Veronica beccabunga* as a representative of Helodids. In the old restored section, substrate homogeneity and the dominance of mesolithal resulted in low abundances of Parvopotamids as species belonging to this growth form prefer finer organic substrates for rooting in the river bottom. Furthermore, the low percentage of shallow bankside areas accounted for the low number of Helodids compared to the young restored sections. *Fontinalis antipyretica* specific for non-restored and the old restored section reflected the presence of artificial substrates, e.g. riprap, as this species is an epiphyte mainly attached to large stable stones.

Benthic invertebrate and fish assemblages did not separate between the non-restored, the young restored sections and the old restored section; especially for benthic invertebrates, dissimilarities between samples were low. Low effects of restoration on benthic invertebrates were recently discussed by several authors (Lepori et al., 2005; Palmer et al., 2010; Jähnig et al., 2011; Haase et al., 2013) and related to multiple pressures on regional or catchment scales, e.g., water pollution or agricultural land use. Several authors emphasized the importance of source populations for recolonization of restored sections in the immediate surroundings (Lake et al., 2007; Jähnig et al., 2010; Verdonschot et al., 2013) and pointed out a distance of 5 km for successful recolonization (Sundermann et al., 2011b). In general, some Ruhr tributaries feature source populations (Dahm et al., 2013), but in the immediate surroundings they are missing. However, young restored sections did not differ much from all other sections, although the construction works of restoration measures changed habitats on the river bottom. This revealed fast colonization by species present in the non-restored sections upstream and underlined the importance of source populations in the immediate surroundings. Corresponding to the absence of clear restoration effects, we did not find indicators for the status of samples sections. Using indicator species analysis, we detected *Gammarus pulex* as typical for non-restored and young restored sections. The absence of coarse particulate organic matter, especially in the sample sections downstream from the Möhne tributary, seemed to be the limiting factor for colonization by *Gammarus pulex* as it is a shredder and, therefore, dependent on the presence of this substrate. It may also reveal a shift in functional lotic communities due to the change of river type from a mid-sized to a large mountain river (Vannote et al., 1980).

Also for fishes, we did not detect clear restoration effects, but differences in compositions up- and downstream from the Möhne tributary. In general, low responses of fishes to restoration were observed by several authors (Lepori et al., 2005; Jähnig et al., 2011). Lake et al. (2007) and Stoll et al. (2013) pointed out that colonization of restored sections mainly originates from the surroundings and depends, therefore, on the regional species pool. In general, fishes are known as good dispersers (Fausch et al., 2002), but water management structures, e.g., weirs and reservoirs, often disrupt the river continuum and, therefore, natural dispersal and migration of fishes (Lake et al., 2007). Although many restoration measures aim at improving longitudinal connectivity by removal of weirs or creation of fish passages, river systems are still fragmented and species pools impoverished (Stoll et al., 2013).

In sample sections upstream of the Möhne mouth, which are under natural conditions attributed to the grayling zone, several typical species inhabited non-restored and young restored sections likewise. This suggested a less impoverished species pool in the upper Ruhr. High abundances of young-of-the-year fishes revealed strong reproduction which might mainly occur in the young restored sections as shallow bankside areas with low current offer spawning areas and refuges for juvenile fishes (Schiemer et al., 2001, Lorenz et al., 2013). Sample sections downstream from the Möhne mouth are attributed to the upper barbel zone which is under natural conditions characterized by higher species richness than the grayling zone. However, downstream sections were inhabited by the same species with obviously lower abundances of both young-of-the-year and adult fishes suggesting three factors inhibiting successful colonization. First, the water temperature in the Ruhr decreases abruptly due to the Möhne confluence which is fed by a reservoir located 11 km upstream from the Möhne mouth. This may act as a barrier for downstream migration of fishes from the young restored sections to the old restored section. Secondly, source populations may be missing in the Möhne river and in the lower Ruhr. Thirdly, if source populations are present in the lower Ruhr, a weir, which is located 7.5 km downstream from the old restored section, may disrupt longitudinal connectivity and inhibit upstream migration from the lower Ruhr to the old restored section.

The eel (*Anguilla anguilla*) was significantly more abundant in non-restored sections and the old restored section due to the presence of artificial embankments composed of large cobbles. Eels hide in the interstice volume between the large cobbles at daytime.

4.5.2 Restoration effects on the riparian zone and potential of indicator species

Restoration strongly improved riparian habitat diversity resulting in obvious benefits for carabid beetles and floodplain vegetation supporting the hypothesis. As expected, changes in habi-

tat and carabid assemblages depend on the timescale as virgin habitats of the young restored sections were colonized by riparian carabids with high dispersal ability and pioneer/ruderal plant species. The old restored section offering a diverse array of habitats is additionally colonized by carabid species with lower dispersal ability and a diverse array of competitive, hygrophilous and perennial plant species.

Restoration created a diverse array of meso- and microhabitats, e.g., floodplain areas and gravel bars which are typical for natural sections of mountain rivers. Riparian microhabitats differed strongest between non-restored and young restored sections mainly due to the construction works in terms of excavation of gravel banks and gravel input. In the old restored section, gravel was still present, but finer mineral and organic substrates enriched resulting in a habitat mosaic comprising gravel bars in transient areas, floodplain areas in which organic substrates accumulated, and islands. The higher elevated areas of islands were less flooded and dead wood, plant remains and finer mineral substrates accumulated.

Carabid beetles responded strong and fast to restoration measures compared to the other organism groups. Differences in carabid assemblages obviously reflected differing habitat composition of non-restored sections, young restored sections and the old restored section, as the presence and local distribution of carabid species depend on properties of substrate and moisture conditions (Andersen, 1978) and vegetation density (Van Looy et al., 2005). In general, restored sections were colonized by a diverse array of species with a dominance of riparian specialists, mainly belonging to the genus *Bembidion*. These species are well-adapted to dynamic riparian areas underlying flood disturbance because of their small body size, flattened bodies and well-developed wings and flight-muscles (Desender & Turin, 1989). The resulting high dispersal ability emphasized by Den Boer (1990b), Marggi (1992) and Günther & Assmann (2005) characterizes them as fast colonizers of new habitats. The strong effects of restoration on carabids and the high importance of dynamic riparian areas were also found by Zulka (2008) who investigated restored riparian habitats in the Austrian Danube floodplain national park. High heterogeneity in riparian habitats, which characterized the old restored section, was composed of a diverse array of habitat templates and yields the potential of a more complex carabid assemblage (Van Looy et al., 2005). The habitat mosaic in the old restored section and resulting diversity in microclimatic conditions featured niches not only for riparian specialists, but also for species typical for vegetated banks, forests and open agricultural land which often have lower dispersal ability, e.g., the wingless species *Pterostichus cristatus*. Wingless carabid species are known to be late colonizers (Lövei & Sunderland, 1996). A high frequency of wingless carabid species in later successional stages was also found by Gobbi et

al. (2007). In general, the changing proportion between winged and wingless carabid species over the investigated timescale indicated ongoing successional processes and underlined the findings of Brandmayr (1991).

In case of the floodplain vegetation, restoration increased species richness and mainly promoted widely distributed grassland and some pioneer species, similar to the results of Rohde et al. (2005). In general, hydrochory (Jansson et al., 2005b) and the soil seed bank (Leyer, 2006), which is composed of viable seeds, fruits, propagules and other reproductive plant structures (Poiani & Johnson, 1988), are the major dispersal strategies of typical floodplain plants. Both strategies are often limited by the lack of source population as near-natural river sections offering propagule sources and floodplains accumulating propagules are rare and widespread (Brederveld et al., 2011). Therefore, the presence and abundance of species nearby restored river sections determines colonizing species (Brederveld et al., 2011), which is reflected by the results. Areas in the direct surroundings of the sample sections were characterized by urban and agricultural land use. Therefore, competitive species with strong light preference and often strong dispersal ability by wind were highly frequent and abundant nearby the restored sections and colonized bare habitats in the young restored sections immediately. The presence of source populations upstream from the sample sections, which could provide typical floodplain species dispersed by hydrochory, was not yet investigated. However, the lack of typical floodplain species in the young restored sections revealed a lack of source populations in the upper Ruhr or a high distance to source populations resulting in longer time spans needed for colonization. Contrastingly, the old restored section which is located downstream from the Möhne mouth, was inhabited by a diverse array of competitive plant species, e.g. *Vicia sepium*, hygrophilous plant species, e.g., *Rorippa* ssp. and perennial competitive plant species, e.g. *Barbarea vulgaris*. Plant species assemblages reflected habitat heterogeneity in the riparian zone and suggested the presence of remaining source populations in the Möhne river. Furthermore, the section might have benefitted from the long time span of 18 to 20 years.

4.5.3 Magnitude of restoration effects on aquatic and riparian habitats and species assemblages

As expected, the magnitude of restoration effects differs between organism groups. Aquatic organism groups showed slower and weaker responses to restoration than riparian organism groups exceptive aquatic macrophytes. The differing responses of organism groups to restoration measures revealed that the creation of habitats was not the only factor for a successful

colonization. Organism groups differ in their dispersal ability and sensitivity to multiple factors, e.g., longitudinal connectivity and the presence of nearby source populations.

The combination of improved riparian habitats and high dispersal ability of carabid beetles resulted in fastest and strongest reactions of this organism group. Although there is a lack of knowledge about the presence of carabid populations in the surroundings of the investigated sections, it could be suggested that species pools of carabid beetles are less impoverished than for aquatic organism groups. Field observations showed that riparian specialists were still present in small patches of bars in non-restored sections which occurred sometimes during low flow conditions in summer. The presence of these stepping stones may enforce the high dispersal ability of riparian carabids. The factor time plays an important role for species compositions of carabid beetles, floodplain vegetation and aquatic macrophytes determining colonization patterns in the short- and the long-term.

The missing responses of benthic invertebrates and fish to restoration and the early effects on floodplain vegetation underlined the findings of Sundermann et al. (2011b), Stoll et al. (2013) and Brederveld et al. (2011), who all observed colonization or restored sections mainly being determined by the species pool in the immediate surroundings. For benthic invertebrates, the minor improvement of aquatic habitats in restored sections might be another factor inhibiting successful colonization as suggested by Jähnig et al. (2008) and Miller & Kochel (2010).

Due to their high sensitivity to multiple stressors, benthic invertebrates and fishes might require longer time spans as investigated to develop in direction of near-natural assemblages. Furthermore, it is difficult to detect clear temporal effects using the investigated sample sections as both, benthic invertebrates and fish are additionally affected by the change of river type between the young restored sections and the old restored section.

4.6 Conclusion

The results of this study delivered good insights into the differing responses of aquatic and riparian organism groups to restoration and the relevance of the factor time. Furthermore it revealed which factors inhibit successful colonization. The fast and strong responses of carabid beetles, aquatic macrophytes, and floodplain vegetation to changing habitat conditions in restored sections illustrated the ecological effectiveness of restoration measures. Furthermore, it emphasizes the potential of these organism groups to detect early restoration effects, but also ongoing successional processes in the floodplain.

The missing or minor responses of benthic invertebrate and fish assemblages to restoration in both timescales suggested several demands for future restoration measures. First, restoration should focus on a stronger improvement of aquatic microhabitats. In case of mountain rivers,

it should aim at high substrate, current and depth variability which could be promoted by the installation of deadwood. Second, distances to source populations and potential barriers should be considered in the positioning of restoration measures. Especially in impoverished catchments with less remaining source populations, the positioning of restored sections in accessible distance to source populations and the consideration of pressures at the catchment level might promote the success of restoration. Third, the study gives strong hints for the importance of the factor time and revealed that longer time spans should be considered, especially for organism groups with lower dispersal abilities and higher sensibility to pressures mentioned above. However, the survey design restricted the analyses of timescales as young restored sections were compared with an old restored section which is influenced by the Möhne mouth and developed passively over a time span of 18 to 20 years. Therefore monitoring over longer time spans is needed to analyze, in which direction restored sections develop over time. Nevertheless, the dataset builds a complex basis for further and detailed analysis of successional patterns within the young restored sections as investigations are still continued, and bears the possibility to analyze interactions between sample sections.

5 Restoration measures and success(ion) in the Lahn river and floodplain: effects on river morphology, local species pool, and functional composition of three organism groups

5.1 Introduction

River restoration should ideally initiate near-natural dynamic processes, eventually leading to a habitat mosaic of different successional stages (Ward et al., 1999; Ward & Tockner, 2001). As part of the planning phase, the development of dynamic processes should be considered (Jansson et al., 2005a). However, the effects of restoration depend on time and on the magnitude of floods as a main force for the development and maintenance of habitat diversity. Flooding magnitude and frequency influence the time required to observe the first effects of restoration and the long-term balance between rejuvenation and terrestrialization. Consequently, the targets of hydromorphological river restoration are best described by a dynamic guiding image (Palmer et al., 2005), as the objective is not a stable state but a dynamic system of natural rivers and their floodplains. From a conceptual viewpoint and with reference to the habitat heterogeneity hypothesis (Tews et al., 2004), hydromorphological restoration may increase species richness due to additional niches. Functional response groups that are strongly depending on habitat conditions (Díaz & Cabido, 2001) may benefit most, e.g. species groups preferring moisture, patchy vegetation coverage or habitat disturbance induced by floods.

Monitoring the effects of river restoration has strongly focused on groups of aquatic organisms, especially benthic invertebrates. Benthic assemblages, however, are often poor measures of restored river morphology due to simultaneous impacts of water quality, flow regimes and dispersal barriers (Lepori et al., 2005; Roni et al., 2006; Jähnig et al., 2009b; Palmer et al., 2010). From a conceptual viewpoint, the restoration of functional habitats (e.g., dead wood or gravel) may change the functional traits of benthic assemblages (Tullos et al., 2009). The effects of restoration on composition, richness and diversity of riparian assemblages are often pronounced (Gilvear & Willby, 2006; Lambeets et al., 2008a). However, functional responses of riparian organisms may offer a better understanding of disturbance and restoration processes than benthic invertebrates (Merritt et al., 2010; Lambeets et al., 2009; Richards et al., 2002; Van Looy et al., 2005).

Overall, there is little understanding of how aquatic and riparian assemblage composition and functional response groups change after river restoration and if these effects persist over time.

Data on restoration effects over longer time spans are still rare, although studies addressing morphology or single organism groups in restored river sections increased steadily in recent years (e.g. morphology: Buchanan et al., 2013, benthic invertebrates: Friberg et al., 1998, Muotka et al., 2002, floodplain vegetation: Baattrup-Pedersen et al., 2000, 2013). However, integrating studies comparing restoration effects on different aquatic and riparian organism groups over time are missing, although organism groups may differ strongly in the recolonization of restored floodplain section. For instance, riparian plants may colonize restored river sections from the soil seed bank (Leyer, 2006), and many riparian carabids are strong fliers and may colonize new habitats rapidly (Den Boer, 1990a; Lambeets et al., 2008b). In contrast, benthic invertebrates include hololimnic species that live exclusively in the water and merolimnic insect species that spend parts of their life cycle outside the water. While hololimnic species mainly disperse by downstream drift over short distances (Turner & Williams, 2000; Elliott, 2003), merolimnic species may disperse actively over larger distances, but the time span available to active dispersal is short compared to carabid beetles.

In this study, we analyze effects of restoration on morphology, benthic invertebrates, floodplain vegetation and carabid beetles in 3 restored sections of the Lahn River, a fourth order mountain river in Germany. We used a control-impact design and compared data obtained 3 to 5 and 7 to 9 years after restoration to analyze the effects of restoration and the temporal differences in instream microhabitats, floodplain mesohabitats, species pools and composition of functional response groups between two sampling events. We tested the following hypotheses:

- Hydromorphological restoration increases habitat heterogeneity of both instream microhabitats and floodplain mesohabitats. Habitat heterogeneity is maintained and promoted by dynamic processes initiated by restoration.
- Hydromorphological restoration creates habitats for additional taxa. Colonization patterns of restored sections over time differ between organism groups depending on dispersal and colonization abilities. Changes in species composition reflect habitat changes over time.
- Hydromorphological restoration supports functional response groups of organisms depending on hydrodynamics, hydrological connectivity, accumulation of organic matter and successional processes. Response time differs between organism groups, with the most rapid response from carabid beetles and the slowest response from benthic invertebrates. Once established the functional composition of the biota is maintained provided that the habitat heterogeneity persists.

In summary, we analyze the morphological and biological processes initiated by the restoration of channel morphology including the stability of newly generated habitats, succession and recolonization.

5.2 Sample sections and field work

5.2.1 Sample sections

We investigated 3 study sites of the mid-sized mountain Lahn River between Bad Laasphe and Marburg in Germany (Figure 5-1; Table 5-1). At each study site, we sampled a pair of one restored section and one upstream non-restored section (500 m maximum distance). Each section was approximately 200 m long. Paired sections were similar in terms of catchment size, catchment land use, river size and slope. Sections were restored between 2000 and 2002.

Table 5-1: Study sites Cölbe, Ludwigshütte, and Wallau of the river Lahn between Bad Laasphe and Marburg: geographic position, catchment area, altitude and the year of restoration.

Site name	Cölbe	Ludwigshütte	Wallau
Latitude [decimal, WGS84]	50.86344	50.92665	50.92858
Longitude [decimal, WGS84]	8.79206	8.49971	8.48703
Catchment size [m ²]	650	288	278
Altitude [m asl]	190	300	300
Restoration year	2000	2002	2001

All three restoration measures aimed to increase habitat heterogeneity (personal information from Herbert Diehl, Bezirksregierung Gießen, the water manager in charge of restoration planning) as the river channels were straightened (Figure 5-2), bordered by fixed embankments and characterized by homogeneous substrate, depth and flow condition. To initiate bank side erosion, bank fixations were removed. Moreover, multiple channels were created doubling the overall width of active channels (Figure 5-3). To activate floodprone areas and enable sediment relocation in riparian zones (Figure 5-4), the entrenchment depth was lowered (Cölbe) and upper soil layers were excavated (Wallau and Ludwigshütte).

The river gauge site ‘Biedenkopf’ (Figure 5-1b), located between the study sites Cölbe and Wallau, served as the hydrological reference for flood events and associated habitat turnover. It is a hydrological station of the Regional Environmental Authority of Hesse (Germany) continuously measuring water level and providing discharge data publicly.

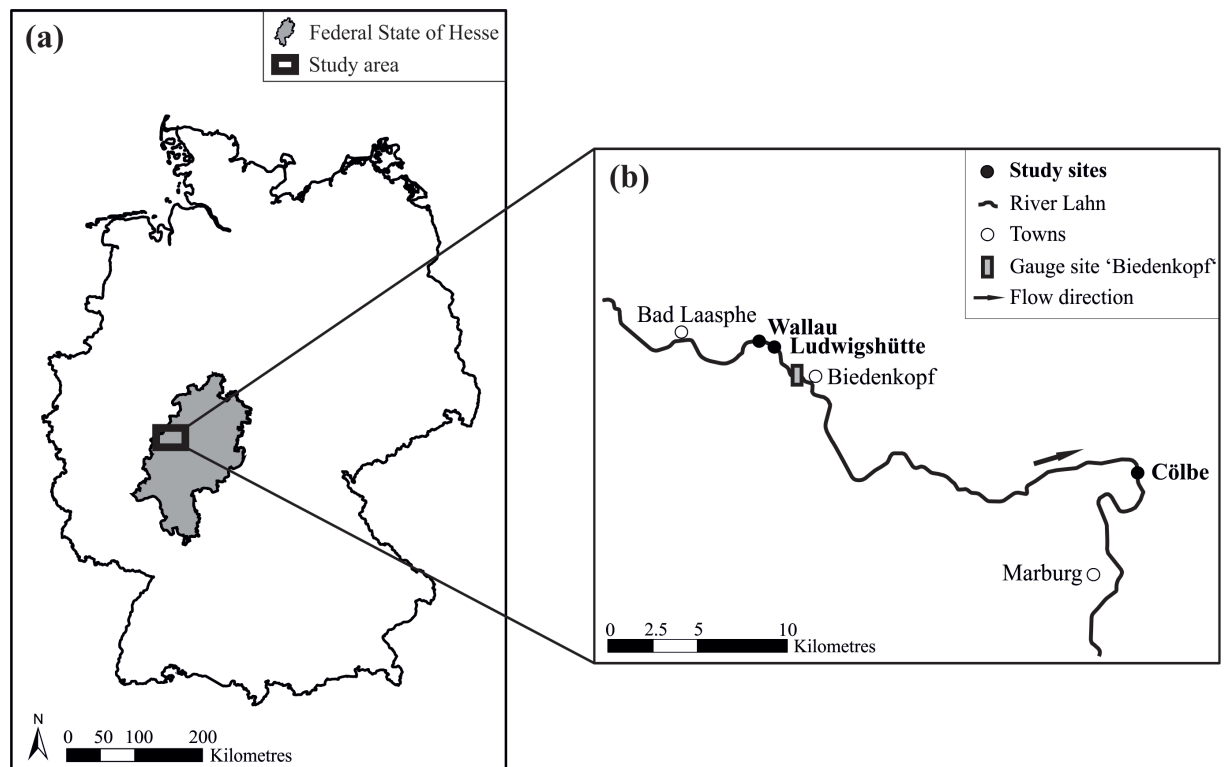


Figure 5-1: Position of the study area in the Federal State of Hesse, Germany (a), position of the study sites, nearby towns, and the gauge site 'Biedenkopf' (b).



Figure 5-2: Picture of a straightened river channel using the example of the degraded section 'Wallau' (June 2009); degraded section reflects the condition of restored section before implementation of the restoration measure.



Figure 5-3: Aerial picture of the restored section 'Ludwigshütte' showing created multiple-channels and widened river channel (A. Lorenz, April 2007).



Figure 5-4: Picture of the restored section 'Cölbe' showing instream and floodplain habitat diversity (June 2009).

5.2.2 Sampling design

We sampled the 3 study sites twice: 2005 (3 to 5 years after restoration) and 2009 (7 to 9 years after restoration), resulting in 12 samples (3 sites x 2 sections x 2 sampling events) per object of investigation. For each of the 12 samples, we investigated instream microhabitats, floodplain mesohabitats, benthic invertebrates, floodplain vegetation and riparian carabid beetles. For each organism group, we analyzed missing and additional taxa and functional response groups. These parameters were analyzed according to differences between the four sample groups ‘non-restored 2005’, ‘restored 2005’, ‘non-restored 2009’ and ‘restored 2009’ (hereafter referred to as sample group comparisons) whereas each sample group contains three samples, each per study site:

- Non-restored sections 2005 vs. non-restored sections 2009, showing **temporal changes in non-restored sections**;
- restored sections 2005 vs. restored sections 2009, showing **temporal changes in restored sections**;
- non-restored sections 2005 vs. paired restored sections 2005, showing **restoration effects after 3 to 5 years**;
- non-restored sections 2009 vs. paired restored sections 2009, showing **restoration effects after 7 to 9 years**.

We calculated temporal changes in non-restored and restored sections as differences between each of the three non-restored and each of the three restored sections separately; for restoration effects we compared each of the three study sites separately. For each sample group comparison, we calculated the arithmetic means of differences.

5.2.3 Field work

Riparian meso- and microhabitats were surveyed once in June and July 2005 and 2009 under low flow conditions along ten transects per river section with an equal distance of 20m spanning the area between the top edges of the embankment. We recorded aquatic and riparian mesohabitats partly based on Raven et al. (1997) and Jähnig et al. (2008) and measured their lengths along the transects to determine the proportion of habitats per river section. Aquatic microhabitats were recorded at 10 points per transects, equally distributed within the aquatic channel features. Detailed information about recording morphology and the data preparation is given in chapter 2.1. Benthic invertebrates were sampled using a multihabitat-sampling design (Meier et al., 2006). For floodplain vegetation and carabid beetles, we used a grab-

sampling method. Detailed information about sample methods of organism groups and the preparation of taxalists is given in chapter 2.2.

5.3 Data processing and analyses

5.3.1 Discharge patterns

Based on the daily mean discharges from November 2004 to November 2009 (hydrological years 2005 to 2009) at the gauge ‘Biedenkopf’, we calculated the mean high flow (MHQ) as the arithmetic mean of the maximum discharges in each hydrological year. We analyzed the frequency of flood events for each year, especially in the hydrological years before the sampling dates (2005 and 2009), as flood events promote habitat turnover and changes in species composition and functional response groups (Wagner et al., 2000).

5.3.2 Instream microhabitats and floodplain mesohabitats

We calculated the mean proportions of habitat types in each of the four sample groups (non-restored 2005, non-restored 2009, restored 2005 and restored 2009) according to our sampling design.

For non-restored sections 2005 and 2009, we hypothesized homogenous habitat compositions and low habitat richness without temporal changes as these sections were straightened and bordered by fixed embankments. In restored sections 2005 and 2009, we expected higher aquatic microhabitat heterogeneity than in non-restored sections due to the more diverse current patterns and subsequent accumulation of fine substrates. We further expected increased heterogeneity of floodplain mesohabitats due to the generation of bars, islands, floodprone areas, standing water bodies and secondary channels. We hypothesized that the effects on microhabitat and mesohabitat heterogeneity were preserved by hydrodynamic processes without evident temporal changes in restored sections from 2005 to 2009. Therefore, we expected strong changes of aquatic and floodplain habitat composition due to restoration effects after 3 to 5 years that will be maintained after 7 to 9 years.

5.3.3 Missing and additional taxa

We counted ‘missing’ and ‘additional taxa’ by using the sample group comparisons of our sampling design. As an example, for temporal changes in non-restored sections, ‘missing taxa’ were those recorded in the non-restored samples 2005 but not in the non-restored samples 2009, while ‘additional taxa’ were those recorded in the non-restored samples 2009 but not in the non-restored samples 2005. We calculated the mean number of missing ($\text{Mean}_{\text{miss}}$)

and additional (Mean_{add}) taxa for each sample group comparison. Each sample group contained three samples.

For each organism group, we defined all taxa recorded in the 12 samples as the local species pool and calculated species richness ($\text{Rich}_{\text{pool}}$) in terms of the total number of taxa (Table 5-2).

Table 5-2: Species richness of the local species pool defined as the total number of species recorded in the 12 samples of benthic invertebrates, floodplain vegetation and carabid beetles.

Organism group	Species richness of the local species pool
Benthic invertebrates	120
Floodplain vegetation	226
Carabid beetles	48

We related the arithmetic mean of missing ($\text{Mean}_{\text{miss}}$) and additional (Mean_{add}) taxa to the species richness of the local species pool ($\text{Rich}_{\text{pool}}$) by calculating the percentage of missing (X_{miss}) and additional (X_{add}) taxa for each sample group comparison:

$$X_{\text{add}} = (\text{Mean}_{\text{add}} / \text{Rich}_{\text{pool}}) * 100,$$

$$X_{\text{miss}} = (\text{Mean}_{\text{miss}} / \text{Rich}_{\text{pool}}) * 100.$$

In general, we hypothesized for all organism groups:

- Temporal changes in non-restored sections: a low and uniform percentage of missing and additional taxa due to stable conditions.
- Temporal changes in restored sections: a low percentage of missing taxa, as the overall habitat composition was maintained by the persistence of dynamic processes, and a higher percentage of additional taxa due to an ongoing colonization by taxa.
- Restoration effects after 3 to 5 and 7 to 9 years: a high percentage of additional taxa, reflecting continuous colonization of restored sections.

5.3.4 Indicators for restoration effects and successional processes

We generated four pooled taxalists per organism group, each for non-restored sections 2005, restored sections 2005 and restored sections 2009 by calculating the arithmetic mean of species abundances. We compared pooled taxalists to extract species:

- present in restored sections 2005, but not in restored sections 2005 indicating restoration effects after 3 to 5 years,

- present in restored sections 2009, but not in restored sections 2005 indicating temporal changes in restored sections from 2005 to 2009.

We restricted the lists to taxa with a mean abundance > 2 as rare taxa cannot be used for the indication of habitat conditions. We analyzed taxa due to potential indication of habitat changes in terms of the presence of flooding dynamics and ongoing succession.

5.3.5 Functional response groups

We selected functional response groups related to potential effects of restoration found in literature (Table 5-3 and Table 4-5), in particular increased hydrodynamics, hydrological connectivity, accumulation of organic matter, and succession. Functional response groups for benthic invertebrates were based on www.freshwaterecology.info (Schmidt-Kloiber et al., 2006), for floodplain vegetation on Klotz & Kühn (2002) and Ellenberg (1974, 1996), and for riparian carabid beetles on Gesellschaft für Angewandte Carabidologie (2009). For each functional response group, we calculated the percentages of abundances within each sample and the mean differences between the sample groups following our sampling design. We hypothesized the following response of functional group abundances:

- Temporal changes in non-restored sections: no changes because of stable and homogeneous flow conditions.
- Temporal changes in restored sections: minor due to the persistence of periodic flooding; as an exception, we expected an increased percentage of benthic invertebrates indicating succession due to continuous colonization by macrophytes.
- Restoration effects after 3 to 5 years: no changes in benthic invertebrate functional response groups due to low colonization potential and dispersal ability; increase of most functional response groups of floodplain vegetation and carabid beetles; in contrast, we expected successional indicators to decrease as flooding generate unvegetated habitats.
- Restoration effects after 7 to 9 years: for benthic invertebrates we expected a slight increase in all functional response groups due to slow but continuous colonization; for floodplain vegetation and carabid beetles we expected a response, similar to the effects 3 to 5 years after restoration, due to persistence of periodic flooding resulting in a dynamic equilibrium.

Table 5-3: Parameter groups and associated benthic invertebrate functional response groups.

Parameter group	Parameter	Associated functional response group	Description
Hydrodynamics	Current diversity	Diversity of current preferences	Restoration enhances current diversity (Jähnig et al., 2008) and thus for more diverse habitats for benthic invertebrates. This includes more frequently occurring low flow areas (e.g. in secondary channels; Jähnig et al., 2009a).
Hydrological connectivity	Areas with low flow	Abundance of limnophil species [%]	Restoration creates shallow riparian areas with low current and lentic zones (e.g. in secondary channels; Jähnig et al., 2009a).
Nutrient availability	Accumulation of organic matter	Abundance of species preferring organic matter [%]	Low flow areas act as sinks for organic matter (Speaker et al., 1984) with potential benefits for macroinvertebrate species inhabiting or feeding on CPOM (Negishi & Richardson, 2003).
Succession	Macrophyte refugia	Abundance of phytal species [%]	Instream habitat heterogeneity in terms of depth, current and substrate diversity enhances the establishment of macrophytes (Iversen, 1993; Lorenz et al., 2012) with potential benefits for benthic invertebrates using macrophytes as habitats and refugia (Iversen, 1985).

Table 5-4: Parameter groups and associated vegetation and carabid beetles functional response groups.

Parameter group	Parameter	Associated functional response group		Description
		Floodplain vegetation	Carabid beetles	
Hydrodynamics	Dynamic riparian areas	Abundance of pioneers and stress-tolerant individuals [%]	Abundance of species preferring unvegetated banks [%]	Hydrodynamics promote the presence and consistently recurrence of unvegetated banks (Hughes, 1997) naturally inhabited by pioneer and stress-tolerant plant species (Gilvear & Willby, 2006) and riparian carabids (Lambeets et al., 2009).
Hydrological connectivity	Hydrologically connected floodplain	Abundance of hygrophilous species [%]	Abundance of hygrophilous species [%]	Restoration enhances hydrological connectivity including more frequent flooding of riparian areas with potential benefits for hygrophilous plant (Corenblit et al., 2009) and carabid species (Bonn et al., 2002).
Nutrient availability	Accumulation of organic matter	Abundance of species with high nitrogen indicator value [%]	Abundance of species preferring banks with mud and organic matter [%]	Floodplains are an important natural sink for suspended sediments and nutrients (Kronvang et al., 2007; Nilsson & Svedmark, 2002) which accumulate in floodplains due to restoration. It supports the growth of nitrophilous plant species and the colonization of carabids preferring banks with mud and organic matter.
Succession	Successional processes in riparian areas	Abundance of competitive species [%]	Abundance of species preferring vegetated habitats [%]	A persistent presence of dynamic riparian processes creates a mosaic of seral stages (Ward et al., 2002). If later succession dominates, the portion of competitive plant species and species preferring vegetated habitats is high.

5.4 Results

5.4.1 Discharge patterns

From November 2004 to November 2009, discharge patterns differed strongly between the hydrological years (Figure 5-5); mean daily discharge exceeded the mean high flow (MHQ) of 55 m³/s three times. The mean high flow was strongly exceeded once in spring 2005 before the first sampling with a discharge of 105 m³/s and twice in 2007 (77 m³/s in January and 81 m³/s in August).

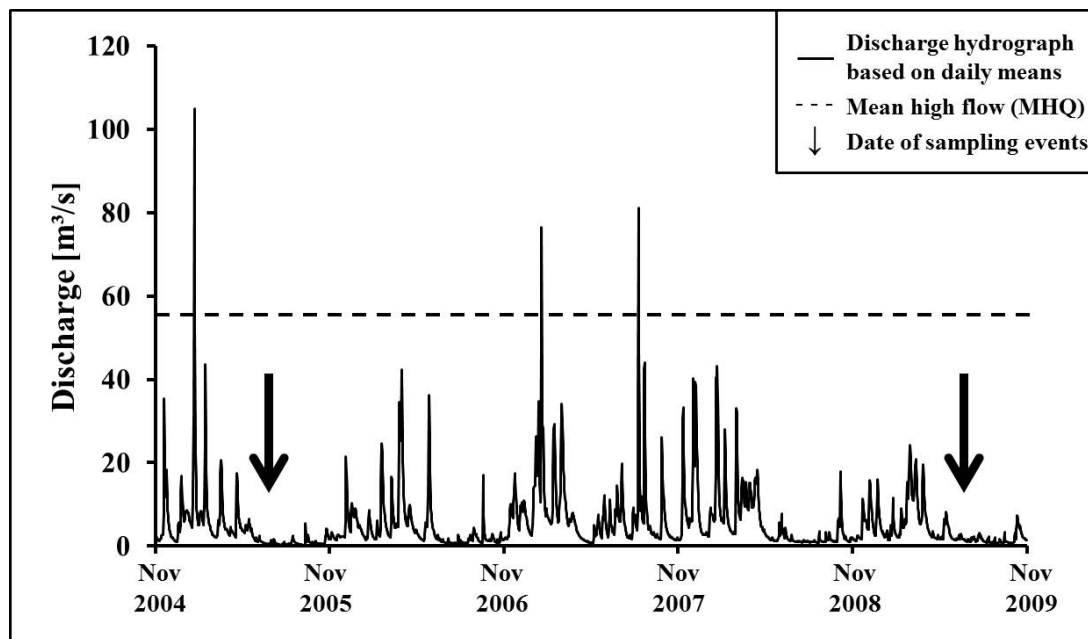


Figure 5-5: Daily mean discharges from November 2004 to November 2009 (hydrological years 2005 to 2009) of the river Lahn at the gauge ‘Biedenkopf’ (hydrological station of the Regional Environmental Authority of Hesse, Germany). Dotted line = mean flood waters mean flood waters (MHQ, Mittlerer Hochwasserabfluss) calculated for the considered time period using the maxima of discharges; arrows = dates of samplings.

In general, the year 2009 was characterized by low flow and a lack of high flood events for nearly all rivers in the Federal State of Hesse; mean discharge for almost all months was below the longtime mean values (Göbel et al., 2010).

5.4.2 Instream microhabitats and floodplain mesohabitats

The instream microhabitats of non-restored sections were mainly cobbles and coarse gravel (95% in 2005 and 96% in 2009) (Figure 5-6); other microhabitats, e.g., finer mineral sediments, organic substrates and floating riparian vegetation were minimally present both in 2005 and 2009, each with less than 3% coverage. In contrast, in restored sections, finer mineral sediments and organic substrates increased in 2005 and 2009 to about 20% coverage,

whereas cobbles and coarse gravel still dominated the river bottom with coverage of around 76%. Submerge macrophytes, tree trunks and dead wood were only present in restored sections in 2005 and 2009, but with low coverage of 0.6 to 1.3%. In conclusion, restoration affected instream microhabitat composition at both sampling dates, but differences between 2005 and 2009 were not detectable in non-restored and restored sections.

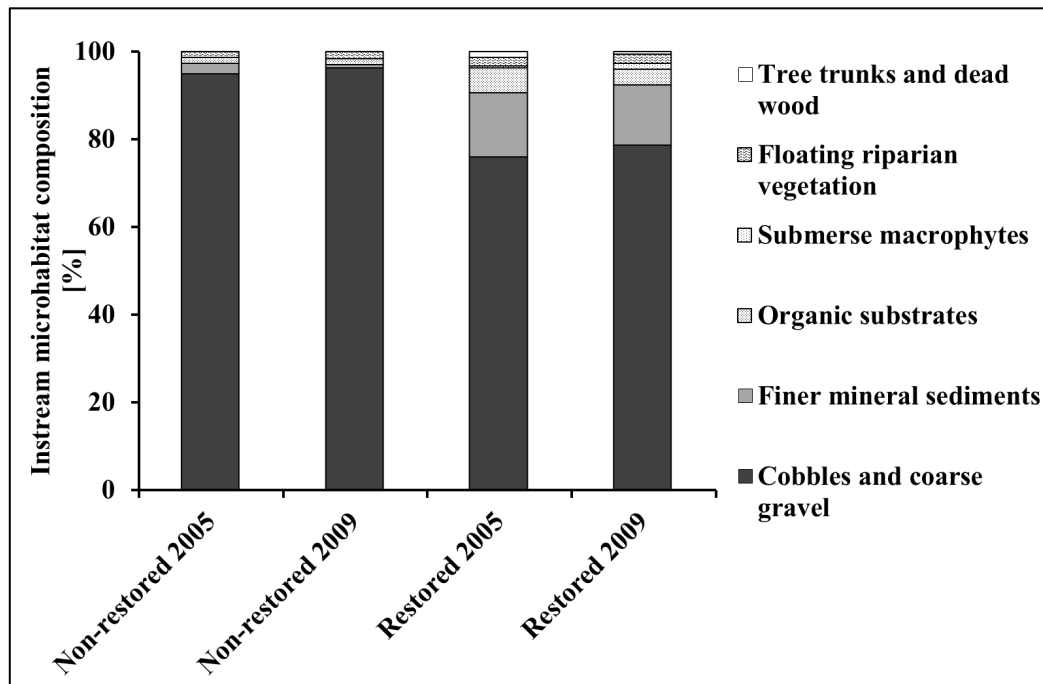


Figure 5-6: Mean proportions of tree trunks and dead wood, floating riparian vegetation, submerge macrophytes, organic substrates, fine mineral sediments, and cobbles and coarse gravel on the river bottom of non-restored and restored sections 2005 and 2009 based on 100 data points per section and sample (100 data points = 100%).

Floodplain mesohabitat composition in non-restored sections was strongly dominated by the mesohabitats ‘main channel’ and ‘embankment and bank’ (> 98%) in 2005 and 2009 (Figure 5-7). In restored sections (2005 and 2009), composition was built up of eight mesohabitat types, with ‘unvegetated bar’, ‘vegetated island’ and ‘moist floodprone areas’ covering nearly 50% of the floodplain area. From 2005 to 2009, composition changed evidently: the proportion of ‘embankment and bank’ nearly doubled whereas ‘unvegetated bar’ decreased half. In conclusion, we detected evident restoration effects on floodplain mesohabitats and temporal changes in restored sections from 2005 to 2009 showing successional processes in riparian areas.

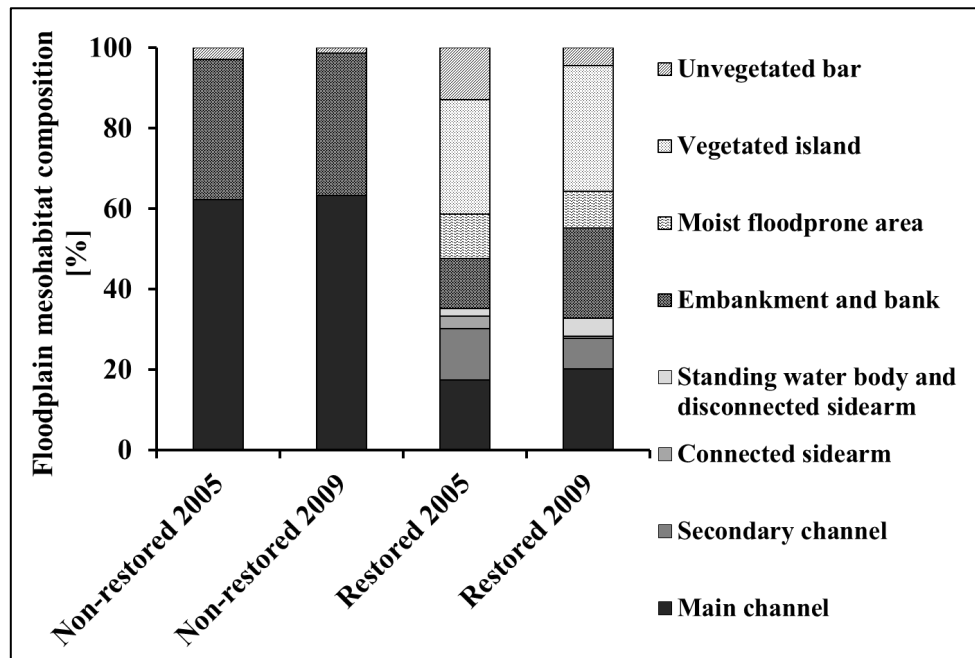


Figure 5-7: Mean proportions of aquatic and riparian mesohabitats of non-restored and all restored sections 2005 and 2009 based on length measurements at ten transects per section and sample (sum of all transect lengths = 100%).

5.4.3 Missing and additional taxa

Species compositions of all organism groups changed only slightly in non-restored sections from 2005 to 2009 (Figure 5-8a); percentages of missing and additional taxa were low with ~10% of the total species number. The exception were benthic invertebrates, for which additional taxa were 10 % higher as missing taxa (total taxa: 120 = 100%; additional taxa: 21 = 17.5%; missing taxa: 9.3 = 7.7%). For temporal differences between 2005 and 2009 in restored sections (Figure 5-8b), a higher percentage of missing and additional taxa (max. 25% of the total species number) was observed. In case of benthic invertebrates and floodplain vegetation, the percentage of missing taxa was about 10% higher than the percentage of additional taxa, while for carabid beetles it was about 8% lower.

Highest percentages of additional taxa varying between 10% and 38% of the total species number were detected for the effects of restoration after 3 to 5 and after 7 to 9 years (Figure 5-8c and Figure 5-8d). These variations in species compositions evidently differed between organism groups and the time period after restoration, especially for additional taxa of floodplain vegetation and carabid beetles. Species composition of both organism groups changed strongly with many additional taxa (27% to 37% of the total species number). Effects of restoration after 3 to 5 years (Figure 5-8c) were stronger for floodplain vegetation than for carabid beetles, while the effects 7 to 9 years after restoration (Figure 5-8d) were stronger for carabid

beetles than floodplain vegetation. In contrast, we observed a low percentage of missing taxa varying between 1% and 10% of the total species number.

In conclusion, we detected evident effects of restoration on additional taxa for floodplain vegetation and carabid beetles; a decrease of missing taxa due to restoration was found for all organism groups. Temporal effects were less obvious, although restored sections showed stronger species fluctuation from 2005 to 2009 than non-restored sections.

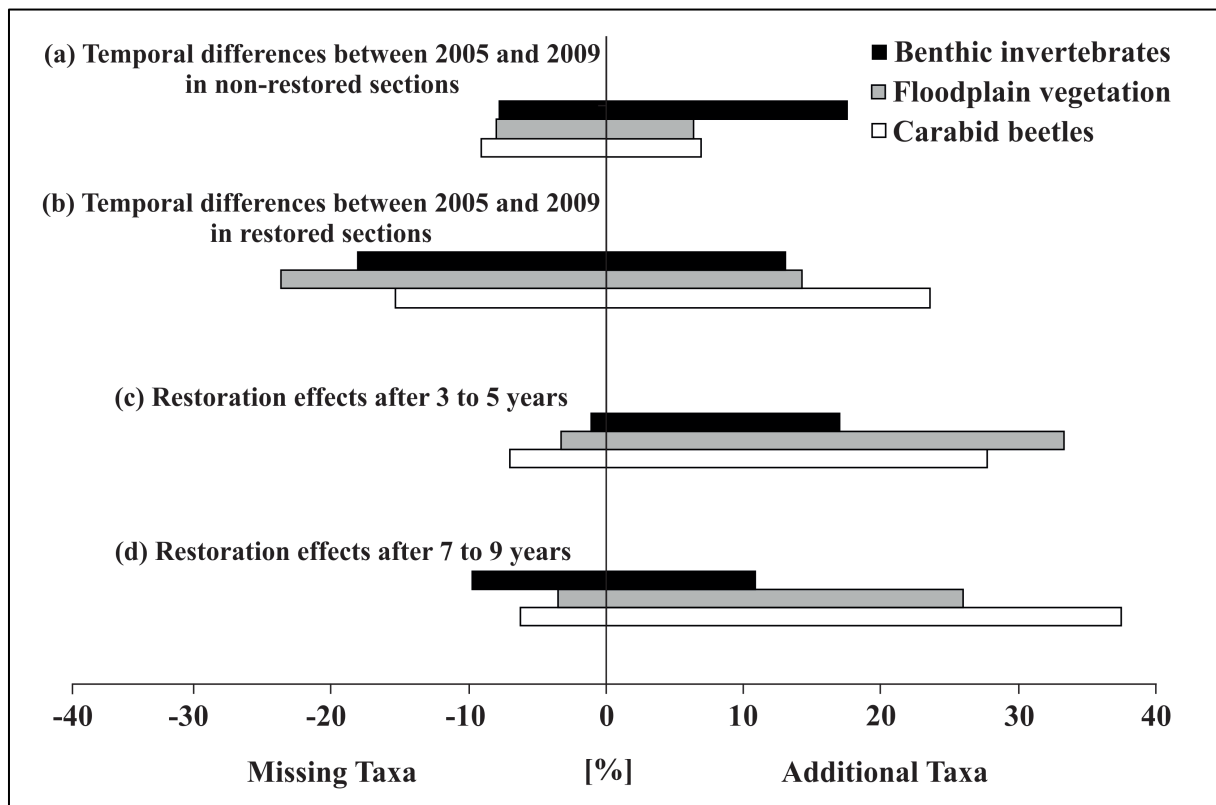


Figure 5-8: Temporal differences in missing and additional taxa of benthic invertebrates, floodplain vegetation and carabid beetles between 2005 and 2009 for non-restored (a) and restored sections (b), and restoration effects after 3 or 5 years (c) and after 7 or 9 years (d). Bars = changes in the mean proportions of missing and additional taxa related to the local species pool (in % of total species number per organism group), calculated pairwise: in case of (a) and (b) for each non-restored and restored section separately, in case of (c) and (d) for each study site separately. Local species pool: for benthic invertebrates 100% = 120 species, for floodplain vegetation 100% = 226 species, for carabid beetles 100% = 48 species.

5.4.4 Indicators for restoration effects and successional processes

In total, 28 species (with a mean abundance > 2) indicated effects of restoration after 3 to 5 years as these species were present in restored sections 2005 but not in non-restored sections 2005 (Table 5-5). Most of these species were carabid beetles (11), followed by plants (10) and benthic invertebrates (7). Especially *Bembidion decorum*, *B. atrocaeruleum* and *Elaphropus*

parvulus were highly abundant in restored sections 2005 with mean abundances were between 89.5 and 123.6 individuals per sample section.

Table 5-5: Indication of restoration effects on species assemblages after 3 to 5 years: additional species found 2005 in restored compared with non-restored sections with their mean abundances (= mean number of individuals per all restored sections in 2005). The table only shows species with mean abundances > 2.

Benthic invertebrates	Ø abundance	Floodplain vegetation	Ø abundance	Carabid beetles	Ø abundance
<i>Hydraena dentipes</i> Ad.	21.0	<i>Saponaria officinalis</i>	5.2	<i>Bembidion decorum</i>	123.6
<i>Ephemera danica</i>	11.1	<i>Glyceria fluitans/plicata/declinata</i>	4.8	<i>Bembidion atrocaeruleum</i>	120.3
<i>Glossiphonia</i> sp.	9.4	<i>Malus sylvestris</i>	4.0	<i>Elaphropus parvulus</i>	89.5
<i>Esolus angustatus</i> Ad.	7.4	<i>Polygonum hydropiper</i>	3.9	<i>Bembidion tibiale</i>	48.6
<i>Odontocerum albicorne</i>	4.2	<i>Galium mollugo</i>	3.9	<i>Poecilus versicolor</i>	27.5
<i>Ceratopogoninae</i> Gen. sp.	4.2	<i>Lamium album</i>	3.7	<i>Bembidion dentellum</i>	7.0
<i>Glossiphonia complanata</i>	3.3	<i>Rumex obtusifolius</i>	2.7	<i>Agonum emarginatum</i>	6.9
		<i>Carduus crispus</i>	2.6	<i>Elaphrus cupreus</i>	5.3
		<i>Ranunculus repens</i>	2.5	<i>Agonum viduum</i>	4.0
		<i>Lamium maculatum</i>	2.1	<i>Pterostichus strenuus</i>	3.5
				<i>Notiophilus palustris</i>	2.5

In the restored sections 2009, 28 species were present which are missing in the restored sections 2005 (Table 5-6), thus indicating successional processes: 12 carabid species, 8 benthic invertebrate species and 7 plant species.

Table 5-6: Indication of temporal differences in species assemblages in restored sections between 2005 and 2009: additional species found 2009 in restored sections compared with 2005 with their mean abundances (= mean number of individuals per all restored sections in 2009). The table only shows species with mean abundances > 2.

Benthic invertebrates	Ø abundance	Floodplain vegetation	Ø abundance	Carabid beetles	Ø abundance
<i>Gammarus fossarum</i>	67.9	<i>Salix triandra</i>	18.3	<i>Carabus granulatus</i>	24.1
<i>Allogamus auricollis</i>	25.9	<i>Salix x rubens</i>	14.5	<i>Bembidion articulatum</i>	16.4
<i>Prosimulium</i> sp.	25.6	<i>Sambucus nigra</i>	5.6	<i>Amara similata</i>	13.1
<i>Halesus digitatus/tesselatus</i>	11.5	<i>Festuca rubra</i>	5.4	<i>Anisodactylus binotatus</i>	9.6
<i>Athripsodes bilineatus</i> ssp.	10.7	<i>Elymus repens</i>	4.8	<i>Loricera pilicornis</i>	6.2
<i>Pedicia</i> sp.	9.6	<i>Rubus caesius</i>	3.6	<i>Agonum fuliginosum</i>	6.2
<i>Brachycentrus subnubilus</i>	6.9	<i>Ribes rubrum</i>	2.1	<i>Patrobus atrorufus</i>	3.5
<i>Limnius perrisi</i> Lv.	2.1			<i>Carabus nemoralis</i>	3.5
				<i>Pterostichus oblongopunctatus</i>	2.3
				<i>Clivina collaris</i>	2.3
				<i>Anchomenus dorsalis</i>	2.3
				<i>Pterostichus anthracinus</i>	2.3
				<i>Nebria brevicollis</i>	2.3

5.4.5 Functional response groups

Abundances of the functional response groups ‘Hydrodynamics’ and ‘Hydrological connectivity’ differed most strongly between 2005 and 2009.

From 2005 to 2009 the abundances of species indicating hydrodynamics (benthic invertebrates and carabid beetles) and of species indicating hydrological connectivity (floodplain vegetation and carabid beetles) decreased in non-restored sections, both about 20%. The abundances of plant species indicating accumulation of organic matter increased slightly (Figure 5-9a). In restored sections, the temporal differences in functional response abundances between 2005 and 2009 were mainly similar to non-restored sections; however, there were three exceptions (Figure 5-9b).

Carabid beetles did not indicate increased hydrological connectivity, but a slight increase in successional indicators (about 5%). Benthic invertebrates indicating succession increased about 10%.

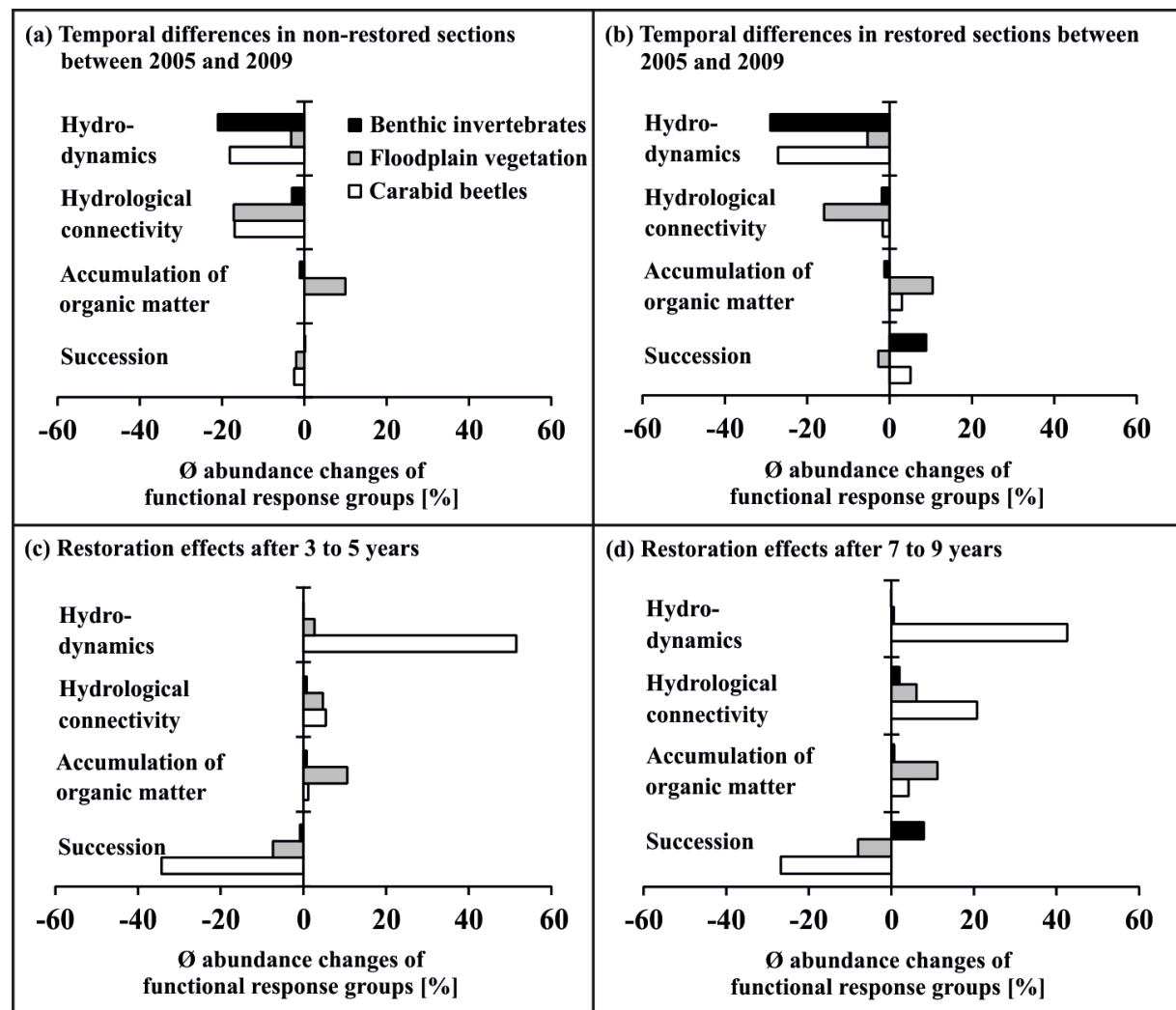


Figure 5-9: Temporal differences in functional response groups of benthic invertebrates, floodplain vegetation and carabid beetles between 2005 and 2009 for non-restored (a) and restored sections (b), and restoration effects after 3 or 5 years (c) and after 7 or 9 years (d). Bars = changes in the mean abundances of functional response groups (in % of the total number of individuals per sample), calculated pairwise: in case of a) and b) for each non-restored and restored section separately, in case of c) and d) for each study site separately.

Effects of restoration after both time periods were strongest for functional response groups of carabid beetles, while effects on floodplain vegetation were minor. 3 to 5 years after restoration abundances of carabid beetles indicating the presence of hydrodynamics (51%) were strongly increased in restored sections compared to non-restored sections while carabid species indicating succession were strongly decreased (35%) (Figure 5-9c). Moreover, we de-

tected minor effects on floodplain vegetation. The abundance of plant species indicating accumulation of organic matter increased about 10%, whereas successional indicators decreased about 7%. Effects of restoration on benthic invertebrates were not observed after 3 to 5 years. Abundance changes of functional response groups 7 to 9 years after restoration were similar to the changes 3 to 5 years after restoration, but with differences in two additional response groups (Figure 5-9d). The abundance of carabid species indicating hydrological connectivity was increased about 20% and the abundance of benthic invertebrate species indicating succession was increased about 8%.

5.5 Discussion

5.5.1 Instream microhabitats

Hydromorphological restoration increased instream habitat heterogeneity supporting our hypothesis, but cobbles and coarse gravel were still dominant in restored sections. Microhabitat composition did not change over time.

Temporal differences of microhabitat composition between non-restored sections in 2005 and 2009 were negligible. These sections were straightened and the riverbed was mainly composed of stones and coarse gravel. Characterized by fixed embankments and homogenous flow conditions, there was no potential to develop habitat heterogeneity.

In restored sections, removing bank reinforcement, lowering the entrenchment depth and creation of multiple channel patterns enabled higher diversity of currents and depths, including shallow banks and pools with low current especially in connected sidearms and secondary channels. These areas promote the accumulation of organic matter and nutrient retention (Lepori et al., 2005; Miller et al., 2010) thus increasing substrate heterogeneity. 3 to 5 and 7 to 9 years after restoration, we detected a more diverse substrate composition in restored than in non-restored sections, mainly composed of stones, gravel, organic matter and finer material typical for near-natural mid-sized mountain rivers (Pottgiesser & Sommerhäuser, 2008). Restored river beds, however, were still dominated by cobbles and coarse gravel. The expected increase of submerse macrophytes was not observed. Rich submerse macrophyte vegetation requires substrate diversity and current and depth variability (Lorenz et al., 2012), preferably with low flow areas where nutrients enrich the sediment (Willby & Eaton, 1996). These conditions developed only in small patches in restored sections.

5.5.2 Floodplain mesohabitats

As expected, restoration increased habitat heterogeneity in the floodplain. This heterogeneity was partly maintained by floods, despite some successional processes.

We found weak differences between non-restored sections 2005 and 2009 as fixed embankments inhibited the possibility of sediment relocation along the banks. These sections consisted of the main channel and embankments; other mesohabitats were hardly present. Though restoration initially increased floodplain area and habitat heterogeneity, the maintenance of dynamic floodplain ecosystems over time depends on sediment relocation by floods (Tockner et al., 2009). In the restored floodplain sections, unvegetated patches were present in 2005, likely due to previous floods in that hydrological year. We expected that floods would preserve unvegetated bars over a time period of 7 to 9 years by also removing early successional stages of vegetation and renewing successional processes (Hughes, 1997). Though this expectation was partly supported, vegetated areas increased, indicating ongoing succession. This buildup of vegetation may have been a result of discharges in the hydrological year 2009, which were significantly lower than in 2005, supporting the progression of successional processes and terrestrialization.

5.5.3 Missing and additional taxa

Supporting our hypothesis, restoration created habitats for additional taxa of benthic invertebrates, floodplain vegetation and carabid beetles. As expected, the time required for colonization of restored sections differed between organism groups. The colonization rate of carabid beetle species in restored sections increased over time, while new plant species appeared stronger 3 to 5 years after restoration. Benthic invertebrates did not respond with increased colonization to restoration and time, but with low and constant species fluctuations between all sample sections.

In non-restored sections, the temporal effects on species composition were minor. These sections were characterized by low habitat diversity in the river and floodplain both in 2005 and in 2009, resulting in small changes in species fluctuation. In restored sections, the overall habitat composition was nearly maintained over time, but there was still a strong fluctuation of species between 2005 and 2009. Changes in species composition of floodplain vegetation and carabid beetles clearly reflected successional processes in the floodplain. This higher variability than found in non-restored sections is typical for riparian ecosystems (Hughes et al., 2005). In the case of benthic invertebrates, species turnover may reflect continuing colonization processes following restoration.

3 to 5 and 7 to 9 years after restoration, the proportion of missing taxa was comparatively low for all organism groups, supporting our expectations that species from non-restored sections colonized nearby restored sections. It could be suggested that restoration stabilized the local species pool of benthic invertebrates by generating lentic habitats, which may act as refugia during high-flow episodes (Negishi et al., 2002). However, the percentage of additional benthic invertebrate taxa in restored sections was as low as in non-restored sections after both time periods. The minor changes in benthic invertebrate assemblages corresponded to the minor changes in instream habitat composition as important microhabitats, e.g. organic substrates or submerge macrophytes were sparse and patchily distributed. In addition, large-scale catchment pressures, the length of restored sections and a lack of nearby source populations may have inhibited the effects of restoration on benthic invertebrates (Jähnig et al., 2009b; Brederveld et al., 2011) as recolonization of restored sections mainly depends on the species pool present in the immediate surroundings (Sundermann et al., 2011b). In contrast, restoration enhanced the species pools of floodplain vegetation and carabid beetles as additional taxa determined up to 38% of the local species pool. Furthermore, the proportion of additional plant and carabid taxa was evidently higher than missing taxa in both time periods after restoration. This supported our hypothesis of ongoing colonization processes in restored sections due to overall habitat heterogeneity in riparian areas. These strong responses may be caused by the superior dispersal abilities of plants and carabids compared to benthic invertebrates. Plants have various means of passive dispersal and riparian carabid beetles colonize newly generated habitats quickly as they have a strong flight ability to explore the availability of new habitats (Den Boer, 1990b; Lambeets et al., 2008b). A positive correlation of flooding and riparian plant species richness was also observed by Baattrup-Pedersen et al. (2013a) for Danish lowland streams. Lambeets et al. (2008a) detected increased richness of carabids on restored lowland river banks. Our results on the floodplain of a mountain river support these findings.

Our hypothesized sequence of recolonization was supported, even if the species pool of benthic invertebrates did not change significantly over time. Floodplain plants colonized the restored sections better than carabid beetles 3 to 5 years after restoration, likely due to colonization from the soil seed bank and the exposure of bare soils in the first years after restoration. Especially the excavation of the upper soil layers in case of the restored sections Wallau and Ludwigshütte may have stimulated the growth of floodplain vegetation as the soil seed bank is its main recolonization strategy (Leyer, 2006). Moreover, Brederveld et al. (2011) showed that short-lived plants with a high production of small, well dispersed seeds were most suc-

successful in colonization 3 to 5 years after restoration. The high discharge in 2005 previous to our investigations may also have stimulated increased colonization. Major parts of the riparian areas were flooded leading to sediment erosion and deposition which is important for setting back succession to pioneer stages (Richards et al., 2002). The renewal of succession normally regards not the whole floodplain (Hughes, 1997). Higher elevated areas, e.g. islands or embankments in restored sections were not affected by flooding and, therefore, dominated by competitive species.

7 to 9 years after restoration, successional processes in the floodplains of restored sections changed species composition due to low discharges in 2009 as local processes and interannual differences in flooding disturbance are the main drivers for changing plant species compositions (Renöfalt et al., 2005). Due to low discharges in 2009, flooding only affected riparian areas directly at the shoreline. The main parts of the floodplain were not disturbed by flooding. Therefore, successional processes determined restoration effects after 7 to 9 year reflected by the decreased share of unvegetated areas. In the increasingly vegetated patches, species compete for light and nutrients and fewer new species appeared. The ongoing succession of floodplain vegetation initiated successional processes of carabid beetle assemblages. It continuously enhanced the local species pool by additional carabid species that prefer vegetated and not necessarily bankside habitats, e.g. *Carabus granulatus* as flight ability is not mandatory for these carabid species (Den Boer, 1990a). Pioneer carabid species were still present in the small unvegetated patches directly at the shoreline.

5.5.4 Indicators for restoration effects and successional processes

In accordance with our analyses of missing and additional taxa, the number of additional taxa newly appearing in restored sections after 3 to 5 years was highest for carabid beetles and plants. The habitat preferences of these species reflected habitat changes due to restoration measures. Species such as *Carduus crispus*, *Ranunculus repens* or *Rumex obtusifolius* (plants) and *Bembidion atrocaeruleum*, *B. decorum* or *Elaphropus parvulus* (carabid beetles) indicated the presence of scarcely vegetated bars in the restored sections 2005. They are well adapted to frequently flooded areas; species as *Ranunculus repens* survives submergence by metabolic adjustment (He et al., 1998); species as *Bembidion atrocaeruleum* escapes quickly from flooded areas by flying (Bates et al., 2006). Plant species, e.g., *Glyceria fluitans* or *Polygonum hydropiper* are hygrophilous (Ellenberg, 1974) and typical for moist floodprone areas (Hubbard, 1942; Sultan et al., 1998) which were created by the restoration measures. Carabid species, e.g., *Bembidion dentellum* or *Agonum emarginatum*, are also hygrophilous (Turin et al., 1991; Luka et al., 2009) with a preference for vegetated habitats (Gesellschaft

für Angewandte Carabidologie, 2009) and reflected, therefore, the presence of vegetated, moist floodprone areas. Although restoration did not enhance the local species pool of benthic invertebrates, we found Ephemeroptera, Plecoptera and Coleoptera species exclusively present in restored sections 2005 (and not present in the non-restored sections 2005). Some of these species, e.g., *Hydraena dentipes* and *Ephemera danica*, are associated to finer mineral sediments (Buffagni et al., 2009) that increased in the restored sections 2005. Aquatic beetles are generally known to be good dispersers (Sanderson et al., 2005).

From 2005 to 2009, the succession of floodplain vegetation in restored sections explained the decreasing share of unvegetated bars and moist areas. Consequently, fewer new species appeared. Additional taxa, e.g., *Salix* sp., *Sambucus nigra* or *Festuca rubra* were mainly competitive (Klotz & Kühn, 2002) and indicated the later successional stages in restored sections 2009. In contrast to plants, carabid beetle species continued to colonize restored sections in 2009. 3 to 5 years after restoration, the species pool was dominated by species preferring unvegetated banks, e.g., *Bembidion atrocaeruleum*, *B. decorum*, and *B. tibiale* (Gesellschaft für Angewandte Carabidologie, 2009). 7 to 9 years after restoration, these species were still present, but accompanied by a high number of specialists on vegetated banks (e.g., *Bembidion articulatum*) and species with a wider range of habitat preferences (e.g., *B. obliquum*) or other moist habitats, e.g., *Carabus granulatus* (forest) or *Amara similata* (pasture).

Although instream microhabitat composition did not differ between 2005 and 2009, new benthic invertebrate species appeared in 2009. The most abundant additional species depended on coarse organic matter, e.g. *Gammarus fossarum* which is an effective leaf shredder (Baldy et al., 2007). Moreover, we found species (e.g. *Halesus digitatus/tesselatus*, *Athripsodes bilineatus*) preferring finer organic and mineral sediments (Graf & Schmidt-Kloiber, 2011). These species reflected the enrichment of leaf litter due to the higher presence of trees and ongoing succession in the restored section 2009. Furthermore it suggested a time-delayed colonization of finer substrates, which had been already present in restored sections 2005.

5.5.5 Functional response groups

In contrast to our hypothesis, organism groups differed not only in response time, but also in their functional response. We expected that hydromorphological restoration supported groups of organisms depending on hydrodynamics, hydrological connectivity, accumulation of organic matter and successional processes as restoration should lead to improved hydrodynamics in terms of bankside erosion and the activation of floodprone areas. These hypotheses were only partly supported by our results.

Although we expected no temporal changes in functional response group composition for non-restored sections, assemblages indicated that there was decreased hydrodynamics (benthic invertebrates and carabid beetles) and decreased hydrological connectivity (floodplain vegetation and carabid beetles). As these differences between 2005 and 2009 were also observed in restored sections, they were likely related to low discharges in 2009.

Effects of restoration after 3 to 5 years were strongest for successional and hydrodynamic indicators among carabid beetles, reflecting changes in floodplain mesohabitat diversity. The presence of unvegetated bars enabled a rapid and strong colonization by riparian carabid beetles as they are highly abundant and strong dispersers (Den Boer, 1970, 1990a). At the same time, the proportion of carabid species preferring vegetated habitats decreased. In contrast to our hypothesis, the functional response of floodplain vegetation 3 to 5 years after restoration was marginal. There was only a weak trend of rejuvenation and accumulation of organic matter, although we detected obvious changes in mesohabitat composition and colonization by additional plant taxa that reflected early successional stages. The overall abundance ratios of functional response groups were not affected by habitat changes. Pioneer species which colonized the riparian areas affected by flooding were low abundant. Competitive species dominated restored sections in abundance as succession could progress in higher elevated areas, e.g. island and embankments.

Contradicting our hypothesis about the effects of restoration after 7 to 9 years, functional response groups of benthic invertebrates did not change, except for successional indicators. Especially Trichoptera species (e.g., *Anabolia nervosa*, *Hydropsyche incognita*, *Mystacides longicornis/nigra*, *M. azurea*) preferring macrophytes as habitats (Graf & Schmidt-Kloiber, 2011) increased in abundance. However, these species were also present in the non-restored sections. This finding suggests that restoration promoted colonization of restored sections from the immediate surroundings in a slow but continuous way. The effects of restoration on functional plant and carabid assemblages after 7 to 9 years were similar to the effects 3 to 5 years after restoration. Although additional plant and carabid species appeared 7 to 9 years after restoration, which indicated progressive succession, the abundances of functional response groups were nearly stable. Pioneer carabid species were still abundant in 2009 although unvegetated habitats had decreased. Additional carabid taxa newly appearing in 2009 and known as colonizers of a wider range of habitats were species-rich but less abundant. Therefore, their appearance did not affect the overall abundance ratios of functional groups.

In summary, our analyses of functional response groups revealed the effects of increased hydrodynamics and early successional stages as indicated by carabid beetles, reflecting some restoration success in terms of ongoing bankside erosion. However, the time-delayed increase of successional indicators of benthic invertebrates reveals the importance of the factor time for recolonization of restored sections. Especially the temporal differences between 2005 and 2009 showed that hydrodynamics and lateral connectivity of the river sections greatly depend on discharge patterns with subsequent impacts on abundances of functional response groups. As these processes are highly variable within and between years, we could not in all cases disentangle the effects of restoration, floods and succession.

5.6 Conclusion

The effects of hydromorphological restoration measures differ between organism groups; the resulting assemblages are subject to subsequent successional processes. Each organism group indicated specific habitat changes or reveal, in case of benthic invertebrates, insufficient changes of instream habitats and the influence of multiple pressures, e.g., the lack of source populations. As floodplain vegetation and carabid beetles showed strongest reactions to changing habitat conditions, we suggest that the assessment of river restoration success should focus on both, the river channel and the floodplain including organism groups.

Monitoring intervals should consider succession, as instream habitats may need time to be formed and colonization by aquatic organisms may require longer time spans. For terrestrial and transient floodplain zones, monitoring should assess whether typical floodplain habitat mosaics are generated initially and maintained over longer time spans. For instance, a persistent increase of floodplain species which indicate the dominance of later successional stages could reveal restoration failure in terms of decreasing habitat heterogeneity over time. Therefore, monitoring over a longer time-period will both help to assess colonization of newly created habitats, and to detect successional processes.

Independent from the morphological river status, functional response abundances of nearly all organism groups indicated temporally changing hydrological conditions due to interannual variability of flooding disturbance. Our survey design with two sampling periods restricted the analyses of linkages between hydrological conditions and biological changes. Nevertheless, the results indicated the importance of discharge variability that may influence restoration success. Therefore, monitoring of restoration effects should consider the discharge regime of a river, but also contain investigations over longer time spans.

6 Summary, conclusions and prospects for future research

This thesis investigated hydromorphological river restoration measures in Germany and their effects on aquatic and riparian habitats and organism groups. Due to the strong alterations of rivers by humans in the last centuries, nearly two third of German rivers lost their natural characteristics (BMU, 2010). The European Water Framework Directive (WFD) claims a good ecological status of all ground and surface waters in the European Union according to chemical, hydromorphological and biological conditions. Therefore, the number of restoration measures strongly increased in the last decade. Aquatic organism groups such as benthic invertebrates and fish, which are used to assess the ecological status, show low or no responses to restoration (Lepori et al., 2005; Roni et al., 2006; Cianfrani et al., 2009; Jähnig et al., 2010; Palmer et al., 2010; Poff & Zimmermann, 2010), although a strong correlation of hydromorphological measures and biotic responses is expected. Several authors pointed out that multiple factors, e.g., agricultural land use, bad water quality (Palmer et al., 2010; Lorenz & Feld 2013; Sundermann et al., 2013) and the lack of source populations (Stoll et al., 2013; Sundermann et al., 2011b) inhibit colonization of restored river sections by aquatic organism groups. Some studies addressed the factor time to be important (Lorenz et al., 2009; Bernhardt & Palmer, 2011; Parkyn & Smith, 2011). However, the knowledge on time spans required for successful recolonization of restored sections is poor. Responses of riparian organism groups to restoration measures are comparatively less investigated, although single studies reveal strong responses to changing habitat conditions (Tockner et al., 1998; Günther & Assmann 2005; Rohde et al., 2005; Lambeets et al., 2008a; Jähnig et al., 2009; Meyer et al., 2010). Furthermore, studies which compare effects of restoration on both aquatic and riparian organism groups are missing, although hydromorphological restoration change habitats in aquatic and riparian zones.

Therefore, the following questions were addressed in this thesis:

- How do riparian organism groups respond to hydromorphological restoration measures?
- How do habitats and species assemblages of the river and the floodplain develop in the first years after restoration and over time?
- How do aquatic and riparian organism groups differ in their responses to restoration measures?

In detail, the following hypotheses were tested:

- (1) Richness and diversity of habitats and species in riparian areas is higher in restored than in non-restored sections.*
- (2) The time since restoration influences habitats and species assemblages in aquatic and riparian areas.*
 - a) Riparian pioneer species and species with high dispersal ability colonize restorations immediately after construction works, whereas aquatic organism groups require longer time spans for developing near-natural assemblages.*
 - b) Habitat heterogeneity in aquatic and riparian areas of restored sections is maintained by dynamic processes enabled by restoration and increase species richness in the long-term.*
- (3) The magnitude of responses to restoration differs between aquatic and riparian organism groups.*

In the first study which focused on hypothesis (1), effects of hydromorphological restoration on riparian habitats and organism groups were analyzed by using the example of carabid beetles and floodplain vegetation for a dataset of 24 restoration measures.

The hypotheses (2) and (3) were both tested in two separate case studies of restoration measures which investigated aquatic and riparian habitats and species assemblages in mid-sized mountain rivers at different time spans after restoration. Thereby, the first case study focused on pioneer colonization in recently restored sections in comparison with colonization of a 20 year old restored section and addressed hypothesis (2a). In the second case study, effects of restoration after 3 to 5 and 7 to 9 years were analyzed addressing the hypothesis (2b).

In the following, the methods, results and main findings of each study with regard to the hypothesis are presented.

1 Effects of river restorations on riparian mesohabitats, floodplain vegetation and carabid beetles

Using the example of 24 restored and nearby non-restored sections in Germany, restoration effects on riparian habitats, floodplain vegetation and carabid beetles were investigated. Riparian habitats were recorded on ten transects per sample section; transects spanned the area between the top edges of embankments. Floodplain vegetation and carabid beetles were investigated on three transects per sample section. For floodplain vegetation, vegetation units and species within the vegetation units were recorded. Carabid beetles were sampled using pitfall traps and hand collections. Based on 18 indices including habitat and species diversity, taxonomic diversity and functional indices, the frequency and magnitude of changes following restoration were analyzed. Riparian habitat diversity doubled in restored sections compared to non-restored sections. The number of vegetation units and plant and carabid beetle species richness also doubled in restored sections, whereas changes in Shannon diversity were most pronounced for mesohabitats and riparian plants. Taxonomic diversity of carabid beetles decreased in restored sections reflecting post restoration dominance of riparian *Bembidion* species. Stress-tolerant pioneers of plant and especially carabid species benefited strongly from the re-establishment of open sand and gravel bars, while hygrophilous species did not respond to restoration. The findings suggest that restoring river hydromorphology has positive effects on riparian habitats, floodplain vegetation and carabid beetles.

Hypothesis (1): 'Richness and diversity of habitats and species in riparian areas is higher in restored than in non-restored sections.'

The hypothesis was supported by the results.

2 Habitat and species compositions in the Ruhr river and floodplain: timescales in restoration effects

In the first case study, habitat compositions in the aquatic and riparian zone and 5 organism groups (benthic invertebrates, fish, aquatic macrophytes, carabid beetles, floodplain vegetation) were investigated in 6 sample sections of the mountain river Ruhr in Germany. We compared habitats and species assemblages between young restored sections, which were stepwise restored from 2007 to 2009, non-restored sections (upstream and downstream of the restored reach) and an old restored section with a passive development since 1990 downstream of all other sections. Investigations started in 2008, the year after the first section was restored, and continued 3 to 5 years. Habitats and riparian organism groups were recorded on

transects, as described in study 1. Sampling of aquatic organism groups was carried out according to the guidelines of the Water Framework Directive.

In the first years after restoration, assemblages of carabid beetles, floodplain vegetation and aquatic macrophytes responded strongly to improved habitat conditions; species richness was obviously higher than in non-restored sections. Riparian carabid beetles with a strong preference for gravel bars and a high dispersal ability colonized newly created habitats immediately. In case of floodplain vegetation, primary settlers were commonly distributed grassland species reflecting colonization from the immediate surroundings. Aquatic macrophytes in young restored sections comprised a diverse array of species with differing traits. Especially Helodids benefitted strongly from the presence of shallow bankside areas. In the old restored section, carabid and plant assemblages were determined by the riparian habitat mosaic. In addition to riparian specialists, carabid species with a broader range of habitat preference were present which are often wingless and have, therefore, lower dispersal abilities. Plant assemblages were composed of competitive, hygrophilous and perennial plant species.

The missing restoration effects of benthic invertebrates and fish might be due to minor restoration effects on instream substrates at the river bottom, the lack of source populations in the immediate surroundings combined with low dispersal ability and, in case of fish, deficits in longitudinal connectivity. Altogether, riparian organism groups and aquatic macrophytes benefited from improved habitat conditions in the short- and the long-term. Benthic invertebrates and fishes might require longer time spans than investigated due to the influence of multiple pressures.

Hypothesis (2a): Riparian pioneer species and species with high dispersal ability colonize restorations immediately after construction works, whereas aquatic organism groups need longer time spans for developing near-natural assemblages.

The hypothesis was mainly supported by the results.

Hypothesis (3): The magnitude of responses to restoration differs between aquatic and riparian organism groups.

The hypothesis was supported by the results.

3 Restoration measures and success(ion) in the Lahn river and floodplain: effects on river morphology, local species pool, and functional composition of three organism groups

At 3 study sites in the mid-sized mountain river Lahn (Germany) temporal effects of restoration on river morphology, on species and functional composition of benthic invertebrates, floodplain vegetation and carabid beetles were investigated. Restored and nearby non-restored

sections were sampled 3 to 5 years and 7 to 9 years after restoration. Habitats and riparian organism groups were recorded on transects, as described in study 1. Sampling of aquatic organism groups was carried out according to the guidelines of the Water Framework Directive. In the restored sections, aquatic substrate heterogeneity was higher than in non-restored sections due to the increased presence of finer substrates; however, cobbles and coarse gravel were still dominant. Aquatic substrate composition did not change between the two sampling events. Riparian areas of restored sections were characterized by a diverse habitat mosaic composed of unvegetated bars, vegetated islands and secondary channels. 7 to 9 years after restoration floodplain habitat heterogeneity in restored sections was maintained, but vegetated areas increased, while unvegetated bars and aquatic areas decreased.

Assemblage compositions of all three organism groups changed over time. Carabid beetles showed the strongest responses to restoration and the most obvious temporal changes, benthic invertebrates the lowest. In general, species richness of plants and carabids was obviously increased in restored sections. 3 to 5 years after restoration, the portion of immigrated species was higher for floodplain vegetation than for carabid beetles. Riparian carabid species, which are well adapted to dynamic habitats and typical for early stages of succession, and a diverse array of pioneer plant species benefited most from increased habitat heterogeneity in riparian areas. 7 to 9 years after restoration, carabid assemblages were enhanced by species which reflect later successional stages leading to increased species richness. In contrast, species richness of floodplain vegetation was decreased due to the development of later successional stages characterized by the dominance of competitive species. Although benthic invertebrate assemblages did not respond clearly to restoration, some species only inhabited the restored sections. This reveals a very slow colonization of restored sections.

Temporal changes of functional groups within the non-restored and the restored sections suggested a decrease of dynamic processes and of lateral connectivity between the river and its floodplain. This might be due to a lack of high discharges in the year prior to the investigation 7 to 9 years after restoration.

Hypothesis (2b): Habitat heterogeneity in aquatic and riparian areas of restored sections is maintained by dynamic processes enabled by restoration and increase species richness.

The hypothesis was partly supported by the results.

Hypothesis (3): The magnitude of responses to restoration differs between aquatic and riparian organism groups.

The hypothesis was supported by the results.

Conclusions

Restoration effects differed between aquatic and riparian, but also between the individual organism groups. For these differences, the impact of multiple factors is suggested, e.g., the magnitude of habitat generation, dispersal abilities of organism groups, the presence of source populations and accessibility of restored sections for dispersing species.

First, morphological river restoration measures increased habitat diversity mainly in riparian areas with strong benefits for riparian organism groups. Species richness increased and, in general, stress-tolerant and pioneer species well adapted to dynamic riparian areas were supported. Riparian carabid beetles are fast colonizers resulting from their flight ability. The generation of gravel bars in mountain rivers, which are indicative for natural conditions of this river type, provided habitats for specialized riparian carabid species. The strong responses of these species to morphological changes render them suitable indicators for morphological restoration measures.

Floodplain vegetation also responded to habitat improvement, but the colonization of floodplain vegetation is highly influenced by the presence of commonly distributed species in the direct surroundings. This may result from lower dispersal ability because they are passively dispersed and reproduce from the soil seed bank. Thereby, the lack of typical floodplain species and impoverished soil seed banks in degraded floodplains may retard the development of near-natural plant assemblages. However, the development of near-natural floodplain vegetation in restored sections benefits from longer time spans and could be accelerated by initial plantings, especially in degraded catchments.

Second, a minor enhancement of substrate diversity on the river bottom combined with low dispersal ability and the lack of source populations in the direct surroundings might inhibit responses of benthic invertebrates and fish. In contrast, aquatic macrophytes react fast and strong to restoration. For them, shallow bankside areas have a high importance as propagules can accumulate in these areas resulting in fast colonization of restored sections subject to the condition that source population upstream from restored sections are present. Although aquatic macrophytes are mainly passively dispersed by hydrochory, they have the ability to disperse over longer distances compared to the active dispersal of benthic invertebrates which is normally effective over short distances.

Third, time is an additional factor influencing colonization of restored sections. Differing dispersal abilities of organism groups result in different time spans required for colonization of newly created habitats. Organism groups with high dispersal ability, e.g., riparian carabid beetles, are direct colonizers, whereas aquatic organism groups suffering from multiple pres-

tures need more time to reach restored sections. Thereby, a high distance to source populations and deficits in longitudinal connectivity might retard or inhibit colonization of restored sections.

Furthermore, the discharge regime of a river across longer time spans influences the development of restored sections. In case of mountain rivers, characterized by natural flooding dynamics and a long-term balance between rejuvenation and terrestrialization, the lack of flooding might lead to decreased habitat diversity as habitat disturbance is a key factor for structuring biotic communities. In the floodplain, processes of terrestrialization and later successional stages dominate and homogenize habitats due to the loss of sediment relocation. However, rivers are characterized by interannual variability of flooding magnitude and frequency. In general, strong flood events reshape habitat conditions in direction of near-natural characteristics and maintain habitat heterogeneity. If such strong flood events are missing in the year before investigations, increased habitat homogeneity in the river and succession in the floodplain reveal a retrogressive development in direction of degraded and straightened river sections. Therefore, it is difficult to pre-estimate in which direction restored river sections develop using one-time investigations.

Prospects for future research

Missing or mixed restoration effects on aquatic organism groups often frustrate policy makers and water managers, but the strong responses of riparian organism groups, especially carabid beetles, may clarify that restoration has positive effects already in the first years after restoration. It would be important to build bridges between aquatic and terrestrial ecology to make limnologists, water managers and policy makers aware of the strong connections between rivers and their floodplains and potential benefits of restoration for both components of a river ecosystem.

To quantify restoration effects on aquatic and riparian biota, a standardized assessment system is needed focusing on both the rivers and their floodplains. The assessment systems of aquatic organism groups used in the monitoring of the ecological status according to the Water Framework Directive seems not to be suitable for detecting restoration effects as chosen metrics are more sensible to general degradation and saprobic pollution than to morphological changes. A nearly finished project (FKZ-371024207) financed and supported by the German Federal Environmental Agency developed an assessment system for restoration success using aquatic organism groups and integrating multiple factors, e.g., morphological degradation, organic pollution, distance to source populations and dispersal abilities of organism groups.

However, a similar system for riparian organism groups is still missing. Data on the effects of restoration measures on riparian organism groups in Germany is scattered, although there seems to be a large number of unpublished investigations. Therefore, there is a strong need to collect all available data. A first step in collecting data and developing a biotic assessment system for floodplains will be done in a project (FKZ-3513850400) financed and supported by the Federal Agency for Nature Conservation. Similar to rivers which are classified in river types due to environmental conditions such as ecoregions, altitude, stream size and catchment geology (Lorenz et al., 2004), floodplains differ in their characteristics which determine shapes of habitats and, therefore, species assemblages. The classification of floodplain types by Koenzen (2005) will help to identify species indicating type-specific habitat conditions.

The results of this thesis give strong hints how the factor time influences colonization of restored river sections. Further investigations including a continuously monitoring over longer time spans are needed to analyze temporal changes of colonization patterns in the long-term. Therefore, the data of this thesis is an important basis for further temporal analyses as most of the restoration measures analyzed in chapter 3 were revisited in 2013 and the monitoring of the Ruhr is still continuing. Concerning future restoration measures, there is a strong demand in the identification and connection of potential source populations as restored sections are often far away and not accessible for dispersing species. Due to the impact of multiple stressors on the success of restoration, the focus must be expanded to the catchment level.

Future research and success of river restoration can profit from the following:

- Bridges between aquatic and terrestrial ecology should be built to increase awareness of river and their floodplains as a functional unity and of the importance of the factor time.
- Available data on riparian organism groups should be collected as a basis for analyses of distribution patterns, restoration effects and source populations in the surroundings of restored river sections.
- A standardized assessment method should be developed to quantify restoration effects on riparian biota including the identification of indicator species specific for different floodplain types.
- Aquatic and riparian organism groups in restored sections should be monitored over longer time spans, in best case following the ‘Before-After-Control-Impact’ design.
- River restorations should preferably be implemented in accessible distance of source populations and built stepping stones for dispersing species.
- Improving river ecosystems should expand the focus on remaining source populations and multiple pressures at the catchment-level.

7 Zusammenfassung

Hintergrund

Flüsse und ihre Auen sind einzigartige Ökosysteme und in ihrer natürlichen Form durch eine Vielzahl unterschiedlicher Habitate charakterisiert (Ward et al., 2002). Dynamische Prozesse in Form von Sedimentumlagerung, die durch das vorherrschende Überflutungsregime gesteuert werden, führen zu einer hohen räumlich-zeitlichen Variabilität der Habitate (Ward et al., 1999; Robinson et al., 2002). Dies macht Flüsse und ihre Auen zu Hotspots der Biodiversität und zu wichtigen Lebensräumen für eine Vielzahl speziell angepasster Pflanzen und Tierarten (Ward et al., 1999; Tockner et al., 2009).

Seit dem Mittelalter unterlagen Flüsse und ihre Auen zunehmend der Nutzung durch den Menschen. Sie wurden begradigt, z.B. für die Schifffahrt (Millennium Ecosystem Assessment, 2005) und wiesen zusätzlich über Jahrzehnte eine schlechte Wasserqualität auf. Die Wasserqualität der deutschen Gewässer hat sich in den letzten Jahrzehnten jedoch deutlich verbessert, so dass nur noch 34% der Gewässer in Deutschland organisch belastet sind (BMU 2010). Die Begradigung und Befestigung der Gewässer und deren Ufer, der Verlust der Durchgängigkeit im Längsverlauf und veränderte Abfluss- und Sedimentbedingungen sind heutzutage die Hauptfaktoren, die die Entwicklung artenreicher Lebensgemeinschaften in Gewässern negativ beeinflussen. Eine bundesweite Studie in Deutschland machte deutlich, dass aktuell ca. 68% der Gewässer strukturell verändert sind (BMU, 2010). Für die Flussauen in Deutschland trifft dies auf ca. 90% zu (BMU & BfN, 2009).

Im Jahr 2000 wurde die Europäische Wasserrahmenrichtlinie implementiert, mit dem Ziel, alle Grund- und Oberflächengewässer bezüglich chemischer, struktureller und biologischer Bedingungen bis zum Jahr 2015 in einen guten ökologischen Zustand zu bringen. Die Bewertung des ökologischen Zustands der Biologie basiert dabei auf Lebensgemeinschaften von Fischen, Makrozoobenthos, aquatischer Makrophyten, Diatomeen und Phytobenthos (Hering et al., 2010). Für die Umsetzung der Wasserrahmenrichtlinie steht die Verbesserung der Gewässerstruktur im Mittelpunkt (EEA, 2012), so dass die Anzahl hydromorphologischer Renaturierungsmaßnahmen stetig zunimmt (Feld et al., 2011). Die erwarteten positiven Reaktionen der Organismen bleiben bislang jedoch häufig aus. Vor allem für das Makrozoobenthos sind oft keine oder nur geringe Effekte festzustellen (Roni et al., 2006; Jähnig et al., 2010; Palmer et al., 2010), während die Reaktionen von Fischen (Lepori et al., 2005; Cianfrani et

al., 2009; Poff & Zimmermann, 2010) und Makrophyten (Pedersen et al., 2007; Lorenz et al., 2012) unterschiedlich ausfallen.

Die Gründe für den ausbleibenden Renaturierungserfolg im aquatischen Bereich sind vielfältig und beinhalten häufig Stressoren auf Einzugsgebietsebene, wie z.B. landwirtschaftliche Nutzung oder organische Belastung der Gewässer (Palmer et al., 2010; Lorenz & Feld 2013; Sundermann et al., 2013). Auch wird kritisiert, dass renaturierte Abschnitte zu kurz sind, um einen positiven Effekt auf Makrozoobenthos-Gemeinschaften zu haben (Jähnig et al., 2010; Haase et al., 2013). Zudem konnte sowohl für das Makrozoobenthos, als auch für Fische nachgewiesen werden, dass das Vorhandensein von Wiederbesiedlungsquellen in der Nähe von renaturierten Abschnitten ein entscheidender Faktor für die erfolgreiche Besiedlung renaturierter Abschnitte ist (Stoll et al., 2013; Sundermann et al., 2011b). Einige Autoren (Lorenz et al., 2009; Bernhardt & Palmer, 2011; Parkyn & Smith, 2011) legen nahe, dass die Besiedlung von renaturierten Abschnitten durch aquatische Organismen längere Zeiträume, als bisher betrachtet, benötigt. Studien, die sich mit der Bedeutung des Faktors Zeit für die Wiederbesiedlung von renaturierten Abschnitten beschäftigen und somit über längere Zeiträume durchgeführt wurden, sind bisher jedoch so gut wie nicht vorhanden.

Ufertypische Organismengruppen, wie z.B. Laufkäfer oder Auenpflanzen, sind hinsichtlich des Erfolges von Renaturierungsmaßnahmen vergleichsweise wenig untersucht. Obwohl die Bedeutung der Auen für aquatische Ökosysteme in Artikel 1 der Wasserrahmenrichtlinie genannt wird, finden Uferlebensgemeinschaften keinerlei Beachtung in der Bewertung des Ökologischen Zustands von Gewässern. Allerdings haben sie ein hohes Potenzial, schneller und stärker auf Renaturierungen zu reagieren als aquatische Organismengruppen, da ihr Vorkommen vor allem an mikroklimatische Bedingungen in der Aue gebunden ist und weniger von überlagernden Faktoren wie Wasserqualität beeinflusst wird. Verschiedene Studien einzelner Renaturierungsmaßnahmen zeigen deutlich, dass ufertypische Lebensgemeinschaften positiv und sehr schnell auf verbesserte Habitatbedingungen reagieren (Tockner et al., 1998; Günther & Assmann 2005; Rohde et al., 2005; Lambeets et al., 2008a; Jähnig et al., 2009; Meyer et al., 2010).

Die Ausrichtung von Fließgewässerbewertungen auf die Organismengruppen im Gewässer sowie das fehlende Wissen über die Relevanz des zeitlichen Aspektes für den Erfolg von Renaturierungen führten zu den folgenden drei Fragestellungen dieser Arbeit:

- (1) Welche Effekte haben strukturelle Verbesserungen von Gewässern im Zuge von Renaturierungen auf Organismengruppen der Ufer und Auen?
- (2) Wie verändern sich die Habitat- und Artenzusammensetzungen im Gewässer und der Aue in den ersten Jahren und langfristig nach Durchführung einer Renaturierungsmaßnahme?
- (3) Wie unterscheiden sich Organismengruppen im Gewässer und der Aue hinsichtlich ihrer Reaktionen auf strukturelle Verbesserungen von Gewässern im Zuge von Renaturierungen?

Aus diesen drei Fragestellungen abgeleitet, wurden im Rahmen dieser Arbeit folgende Hypothesen überprüft:

- (1) *Die Uferbereiche von Flüssen weisen in renaturierten Abschnitten eine höhere Habitat- und Artenvielfalt auf als in nicht-renaturierten.*

Renaturierungsmaßnahmen schaffen eine Vielzahl verschiedener Uferhabitate, z.B. Uferbänke, Inseln und Überschwemmungsbereiche. Diese bilden eine wichtige Grundlage für die Besiedlung durch artenreiche Pflanzen- und Laufkäfer-Gemeinschaften. Pionierarten und feuchtigkeitsliebende Arten profitieren aufgrund ihrer Anpassungen an dynamische Uferbereiche und Überflutung am stärksten von den Habitatveränderungen.

- (2) *Die Zeitspanne seit Durchführung einer Renaturierungsmaßnahme beeinflusst die Habitat- und Artenzusammensetzung im Gewässer und in der Aue.*

- a) *Ufertypische Pionierarten mit hoher Ausbreitungsfähigkeit besiedeln neu renaturierte Abschnitte direkt; Organismengruppen im Gewässer benötigen längere Zeiträume für die Ausprägung typischer Lebensgemeinschaften.*

In den ersten Jahren nach Durchführung einer Renaturierungsmaßnahme bieten neu geschaffene Habitate die Grundlage für Pionierbesiedlung. Nach einer Zeitspanne von 18 bis 20 Jahren sind renaturierte Abschnitte durch Habitatvielfalt gekennzeichnet und von ufertypischen Pionierarten, konkurrenzstarken Arten und von Arten mit geringerer Ausbreitungsfähigkeit besiedelt.

- b) *Die Habitatvielfalt im Gewässer und der Aue renaturierter Abschnitte wird durch dynamische Prozesse aufrecht erhalten und führt langfristig zu einer Erhöhung des Artenreichtums.*

Durch die Entfernung der Uferbefestigung und die Schaffung flacher Ufer sind dynamische Prozesse in Form von Sedimentumlagerung der Gewässersohle und der Uferbereiche möglich. Überflutungsereignisse, die in Deutschland in der Regel im Winter und Frühling auftreten, bewirken das Fortbestehen dynamischer Prozesse und erhalten die neu entstandene Habitatvielfalt langfristig. Dies ermöglicht eine kontinuierliche Besiedlung der Habitate durch im Wasser und am Ufer lebenden Organismen.

- (3) *Die Stärke der Reaktionen auf Renaturierung unterscheidet sich zwischen Organismengruppen im Gewässer und in der Aue.*

Organismengruppen der Ufer und Auen reagieren aufgrund ihrer Ausbreitungsstrategien stärker auf Renaturierungsmaßnahmen. Ufer-Laufkäfer verbreiten sich aktiv durch ihre Flugfähigkeit. Auenpflanzen besitzen eine Vielzahl von passiven Verbreitungsmechanismen, z.B. Wasser-, Wind- und Tierverbreitung, und reproduzieren sich zusätzlich aus der Diasporenbank im Boden. Dagegen ist die Ausbreitung von im Wasser lebenden Organismengruppen in starkem Maße an den Wasserkörper und den Flusslauf gebunden und wird oft durch verschiedene Faktoren negativ beeinflusst.

Der ersten Arbeitshypothese ist eine Studie gewidmet, in der die Effekte von Fließgewässer-Renaturierungen auf Uferhabitate, Auenvegetation und Laufkäfer anhand von 24 Renaturierungsmaßnahmen untersucht wurden. Die Arbeitshypothesen (2) und (3) wurden beide anhand von 2 Fallbeispielen überprüft, basierend auf Untersuchungen von Habitaten und Organismen im Gewässer und der Aue in 2 Mittelgebirgsflüssen, die zu unterschiedlichen Zeitpunkten nach Fertigstellung der Renaturierungsmaßnahmen stattgefunden haben. Dabei beschäftigt sich die erste Fallstudie mit der Pionierbesiedlung neu renaturierter Abschnitte im Vergleich zu einer ca. 20 Jahre alten Renaturierung (Hypothese 2a). In der zweiten Fallstudie wurden Renaturierungseffekte nach einer Zeitspanne von 3 bis 5 und 7 bis 9 Jahren untersucht (Hypothese 2b).

Im Folgenden werden die drei Studien, die Vorgehensweisen, die wichtigsten Ergebnisse sowie die Erkenntnisse im Hinblick auf die Hypothesen dargestellt.

Ergebnisse

1 Auswirkungen von Fließgewässer-Renaturierungen auf Uferhabitate, Auenvegetation und Laufkäfer

Anhand von 24 renaturierten und 24 stromaufwärts gelegenen nicht-renaturierten Fließgewässerabschnitten in Nordrhein-Westfalen, Hessen und Rheinland-Pfalz wurden Renaturierungseffekte auf Uferhabitate, Auenvegetation und Laufkäfer untersucht. Die Kartierung der Uferhabitate erfolgte entlang von zehn Transekten pro Gewässerabschnitt. Die Transekte reichten jeweils von Böschungsoberkante zu Böschungsoberkante. Die Erfassung der Auenvegetation und der Laufkäfer wurde auf drei der 10 Transekte pro Abschnitt durchgeführt. Bei der Auenvegetation wurden sowohl Vegetationseinheiten, als auch Arten innerhalb der Vegetationseinheiten kartiert. Die Untersuchung der Laufkäfergemeinschaften erfolgte mit Hilfe von Barberfallen und durch Handaufsammlungen.

Auf Grundlage von 18 Indizes, die auf Habitat- und Artenreichtum, Diversität, taxonomische Diversität und funktionale Gruppen abzielten, wurden die Häufigkeit und die Stärke von positiven und negativen Renaturierungseffekten analysiert. Die Diversität der Uferhabitate war in renaturierten Abschnitten doppelt so hoch wie in nicht-renaturierten. Gleiches zeigte sich auch für den Artenreichtum der Auenvegetation und der Laufkäfer, wobei Zunahmen in der Diversität am deutlichsten für die Uferhabitate und die Auenvegetation waren. Die taxonomische Diversität der Laufkäfer war in renaturierten Abschnitten geringer als in nicht-renaturierten und spiegelte die starke Dominanz uferbewohnender *Bembidion*-Arten wider. Stresstolerante Pionierarten unter den Pflanzen und Laufkäfern profitierten deutlich von der Wiederherstellung unbewachsener Sand- und Kiesbänke, während hygrophile Arten nicht auf die Habitatveränderungen reagierten. Insgesamt zeigten sich positive Effekte von Renaturierungen auf die Uferhabitate, die Auenvegetation und die Laufkäfer.

Die Hypothese (1) „*Die Uferbereiche von Flüssen weisen in renaturierten Abschnitten eine höhere Habitat- und Artenvielfalt auf als in nicht-renaturierten.*“ wird durch die Ergebnisse unterstützt.

2 Habitat- und Artenzusammensetzung der Ruhr und seiner Aue: Zeitskalen von Renaturierungseffekten

Untersucht wurden 6 Abschnitte am Mittelgebirgsfluss Ruhr in Nordrhein-Westfalen: 3 renaturierte Abschnitte, die zwischen 2008 und 2011 abschnittsweise auf einer Gesamtlänge von 2,7 km renaturiert wurden, sowie 2 nicht-renaturierte Vergleichsabschnitte und ein Abschnitt,

der sich seit 1990 ungestört entwickelt. Über eine Zeitspanne von 3 bis 5 Jahren, beginnend im Jahre nach der ersten Renaturierungsmaßnahme, fanden Transekt-basierte Kartierungen von Habitaten im Gewässer und in der Aue sowie eine Erfassung von aquatischen (Makrozoobenthos, Fische, aquatische Makrophyten) und uferbewohnenden Organismengruppen (Laufkäfer, Auenvegetation) statt. Die Beprobung der Organismengruppen im Gewässer erfolgte nach den Vorgaben der Wasserrahmenrichtlinie, die der Organismengruppen der Aue wie in Studie 1 beschrieben. Für die Analyse von Renaturierungseffekten und zeitlichen Einflüssen wurde die Ähnlichkeit (Bray Curtis) der Habitat- und Artenzusammensetzungen zwischen den nicht-renaturierten Abschnitten, den jung renaturierten Abschnitten und der alten passiven Renaturierung verglichen.

In den ersten Jahren nach Fertigstellung der Renaturierungsmaßnahmen zeigten sich, im Vergleich zu den nicht-renaturierten Abschnitten, deutliche Unterschiede in der Artenzusammensetzung und ein deutlich erhöhter Artenreichtum für die Laufkäfer, die Auenvegetation und die aquatischen Makrophyten als Reaktion auf die verbesserten Habitatbedingungen. Die neu geschaffenen Habitate, wie z.B. Kiesbänke, wurden direkt von Uferspezialisten der Laufkäfer besiedelt, die aufgrund ihrer Flugfähigkeit ein hohes Ausbreitungspotenzial besitzen. Die Erstbesiedler unter den Pflanzen waren weitverbreitete Pionier- und Graslandarten, die im direkten Umfeld der renaturierten Abschnitte zahlreich vorhanden waren. Bei den aquatischen Makrophyten profitierten vor allem Helophyten von der Schaffung flacher Überschwemmungsbereiche. In der ca. 20 Jahre alten passiven Renaturierung spiegelten vor allem die Laufkäfer, aber auch die Auenvegetation das vorhandene Habitatmosaik in der Aue wider. Neben Uferspezialisten konnten dort Laufkäferarten mit einem breiteren Habitatspektrum und flugunfähige, also ausbreitungsschwache Arten gefunden werden. Die Auenvegetation wies ein breites Spektrum an konkurrenzstarken, feuchtigkeitsliebenden und ausdauernden Pflanzen auf.

Für die fehlenden Renaturierungseffekte beim Makrozoobenthos und bei den Fischen können mehrere Faktoren vermutet werden: eine nur geringe Verbesserung der Substratvielfalt auf der Gewässersohle und das Fehlen von Quellpopulationen in erreichbarer Distanz zu den renaturierten Abschnitten in Verbindung mit einer geringeren Ausbreitungsfähigkeit, die an den Wasserkörper und den Gewässerkorridor gebunden ist. Bei den Fischen, die grundsätzlich eine hohe Ausbreitungsfähigkeit aufweisen, verhindern oft Querbauwerke das Erreichen von renaturierten Abschnitten. Insgesamt profitieren Uferorganismen, aber auch aquatische Makrophyten kurz- und langfristig von der Verbesserung der Habitatbedingungen. Eine deutliche

Verbesserung der Makrozoobenthos- und Fischgemeinschaften benötigt aufgrund der Wirkung verschiedener Faktoren vermutlich längere Zeiträume als betrachtet.

Die Hypothese (2a) „*Ufertypische Pionierarten mit hoher Ausbreitungsfähigkeit besiedeln neu renaturierte Abschnitte direkt; Organismengruppen im Gewässer benötigen längere Zeiträume für die Ausprägung typischer Lebensgemeinschaften.*“ wird durch die Ergebnisse zum größten Teil unterstützt.

Die Hypothese (3) „*Die Stärke der Reaktionen auf Renaturierung unterscheidet sich zwischen Organismengruppen im Gewässer und in der Aue*“ wird durch die Ergebnisse gestützt.

3 Renaturierungen und Sukzession an der Lahn und ihrer Aue: Auswirkungen auf Habitate, Artenpool und funktionale Zusammensetzung dreier Organismengruppen

Anhand von drei renaturierten und jeweils oberhalb gelegenen nicht-renaturierten Vergleichsabschnitten des Mittelgebirgsflusses Lahn in Hessen wurden zeitliche Effekte von Renaturierungen auf die Gewässermorphologie, die Artenzusammensetzung und die funktionale Zusammensetzung des Makrozoobenthos, der Auenvegetation und der Laufkäfer untersucht. Die Probennahmen fanden 3 bis 5 und 7 bis 9 Jahre nach Abschluss der Renaturierungsmaßnahmen statt. Die Kartierungen der Morphologie beinhalteten Transekt-bezogene Kartierungen von Mesohabitaten der Aue und des Gewässers sowie der Substrate auf der Gewässersohle. Die Beprobung des Makrozoobenthos erfolgte nach den Vorgaben der Wasserrahmenrichtlinie, die der uferbewohnenden Organismengruppen wie in Studie 1 beschrieben.

Renaturierte Abschnitte wiesen eine höhere Substratvielfalt auf der Gewässersohle auf als nicht-renaturierte, allerdings dominierte das Substrat Grobkies deutlich. Zeitliche Veränderungen der Substratzusammensetzung konnten nicht festgestellt werden. Die Uferbereiche renaturierter Abschnitte waren durch ein vielfältiges Habitatmosaik bestehend aus Kiesbänken, Inselbereichen und Nebenarmen gekennzeichnet. Die Habitatvielfalt in der Aue war auch 7 bis 9 Jahre nach Fertigstellung der Renaturierung noch vorhanden. Allerdings zeigte sich eine zunehmende Sukzession. Laufkäfer zeigten die stärksten Reaktionen auf Renaturierung und die deutlichsten zeitlichen Veränderungen, das Makrozoobenthos die geringsten. Der Artenreichtum der Pflanzen und Laufkäfer war in den renaturierten Abschnitten höher als in den nicht-renaturierten Abschnitten. 3 bis 5 Jahre nach Umsetzung der Renaturierungsmaßnahmen wiesen die Pflanzen einen höheren Anteil neu auftretender Arten auf als die Laufkäfer. Durch die verbesserte Habitatvielfalt in der Aue wurden zunächst vor allem Laufkäferarten gefördert, die für dynamische Uferbereiche und frühe Sukzessionsstadien typisch sind, sowie eine Vielzahl von Pflanzenarten, die als Pionierbesiedler gelten. 7 bis 9 Jahre nach Um-

setzung der Renaturierungsmaßnahmen erweiterte sich die Laufkäfergemeinschaft um Arten, die das Vorkommen späterer Sukzessionsstadien widerspiegeln. Bei der Auenvegetation beinhaltete die Entwicklung späterer Sukzessionsstadien eine Dominanz konkurrenzstarker Arten und somit einen Rückgang des Artenreichtums. Trotz der insgesamt geringen Reaktionen des Makrozoobenthos konnten in beiden Zeitspannen nach Renaturierung Arten vorgefunden werden, die ausschließlich in renaturierten Abschnitten vorhanden waren. Dies deutet auf eine langsam ablaufende Wiederbesiedlung renaturierter Abschnitte hin.

Die zeitlichen Veränderungen funktionaler Gruppen innerhalb der nicht-renaturierten und der renaturierten Abschnitte zeigten beide eine Abnahme dynamischer Prozesse und eine geringere hydrologische Anbindung der Aue an. Dies lässt auf einen Zusammenhang mit fehlenden Hochwasserereignissen im Jahr vor der zweiten Untersuchung schließen. Insgesamt wurde die durch Renaturierung geschaffene Habitatvielfalt im Gewässer und der Aue aufrechterhalten, jedoch zeigten sich 7 bis 9 Jahre nach Umsetzung der Renaturierungsmaßnahmen Sukzessionsprozesse in der Aue. Vor allem für die Organismengruppen der Ufer konnte eine Erhöhung des Artenreichtums über die Zeit festgestellt werden, während das Makrozoobenthos eine sehr langsame Besiedlung der neu entstandenen Habitate zeigte.

Die Hypothese (2b) *Die Habitatvielfalt im Gewässer und der Aue renaturierter Abschnitte wird durch dynamische Prozesse aufrecht erhalten und führt langfristig zu einer Erhöhung des Artenreichtums.*“ wird durch die Ergebnisse teilweise unterstützt.

Die Hypothese 3 *„Die Stärke der Reaktionen auf Renaturierung unterscheidet sich zwischen Organismengruppen im Gewässer und in der Aue“* wird durch die Ergebnisse gestützt.

Schlussfolgerungen

Die Auswirkungen von Renaturierungsmaßnahmen unterschieden sich vor allem zwischen aquatischen und uferbewohnenden Organismengruppen, aber auch zwischen den einzelnen Organismengruppen. Die Ergebnisse lassen vermuten, dass diese Unterschiede aus dem Einfluss verschiedener Faktoren resultieren, z.B. dem Ausmaß an Habitatverbesserungen, der Ausbreitungsfähigkeiten der Organismengruppen, dem Vorhandensein von Quellpopulationen und der Erreichbarkeit der renaturierten Abschnitten.

Die untersuchten hydromorphologischen Renaturierungsmaßnahmen zeigten bemerkenswerte positive Effekte auf die Besiedlung der Uferbereiche durch die Laufkäfer und die Auenvegetation. Die Entfernung von Uferbefestigungen, die Schaffung flacher Uferbereiche und damit die Initialisierung von dynamischen Prozessen sind wirksame Maßnahmen, die auch längerfristig zu Struktur- und Habitatvielfalt in der Aue führen. Sie bilden eine wichtige Grundlage

für die dortige Artenvielfalt. Vor allem die Gruppe der Laufkäfer, bei denen die uferbewohnenden Arten aufgrund ihrer Flugfähigkeit hochmobil sind, spiegeln die Verbesserung der Strukturvielfalt, aber auch Sukzessionsprozesse deutlich wider. Die Schaffung und das Fortbestehen von Kiesbänken in Mittelgebirgsflüssen, die diese Flüsse in ihrer natürlichen Form charakterisieren, bietet eine wichtige Besiedlungsgrundlage für eine ganze Reihe spezialisierter Laufkäfer-Arten. Die insgesamt schnellen und deutlichen Reaktionen auf Habitatveränderungen macht Laufkäfer zu guten Indikatoren für erfolgreiche Auenrenaturierungen. Auch die Auenvegetation zeigte insgesamt positive Reaktionen auf die Renaturierungsmaßnahmen. Die Besiedlung renaturierter Abschnitt durch Pflanzen war maßgeblich durch die vorhandenen Arten in direkter Nähe bestimmt wird. Dementsprechend kann das Fehlen von typischen Auenpflanzen in erreichbarer Nähe und die durch die menschliche Nutzung stark überprägten Diasporenbanken im Boden degradierter Auen die Entwicklung einer naturnahen Pflanzengesellschaft verzögern. So sind für eine erfolgreiche Wiederbesiedlung renaturierter Abschnitte durch Auenpflanzen längere Zeitspannen zu erwarten, die vor allem in stark überformten Einzugsgebieten durch Initialpflanzungen beschleunigt werden könnten.

Die geringen oder fehlenden Reaktionen des Makrozoobenthos und der Fische in den beiden untersuchten Fallbeispielen läßt auf drei Hauptfaktoren schließen, die eine erfolgreiche Besiedlung erschweren: die vergleichsweise geringe Verbesserung der Substratdiversität auf der Gewässersohle, die geringe Ausbreitungsfähigkeit, da deren Ausbreitung stark an den Wasserkörper und den Gewässerkorridor gebunden ist, sowie das Fehlen von Quellpopulationen in der Nähe von renaturierten Abschnitten. Im Falle der Fische, die generell für ihre starke Ausbreitung innerhalb von Wasserkörpern bekannt sind, bilden zudem Querbauwerke Wanderhindernisse. Dementsprechend müssen künftige Renaturierungen auf unterschiedlichen räumlichen Skalen ansetzen. Auf der lokalen Ebene ist eine ausreichende Verbesserung der Habitatvielfalt im Gewässer wichtig. Auf der Einzugsgebiets-Ebene sollte das Vorhandensein von potenziellen Quellpopulationen, aber auch von Stressoren miteinbezogen werden. Im besten Fall sollte eine Vernetzung von Restpopulationen durch Renaturierung und eine Aufwertung des gesamten Einzugsgebiets stattfinden. Renaturierte Abschnitte können dabei als wichtige Trittsteine dienen. Im Gegensatz zum Makrozoobenthos und den Fischen zeigten die aquatischen Makrophyten positive Reaktionen auf die untersuchten Renaturierungsmaßnahmen. Aquatische Makrophyten verfügen über eine passive Verbreitungsstrategie über den Wasserkörper, die über längere Distanzen wirkt. Sie profitieren vor allem von der Schaffung flacher Uferbereiche, in denen sich Diasporen anreichern können, vorausgesetzt, dass Quellpopulationen oberhalb des renaturierten Abschnittes vorhanden sind.

Der zeitliche Aspekt stellt einen zusätzlichen Faktor dar, der für eine erfolgreiche Wiederbesiedlung eine bedeutende Rolle spielt. Die unterschiedlichen Ausbreitungsfähigkeiten von Organismengruppen resultieren in unterschiedlichen Zeitspannen, die für eine Besiedlung neu geschaffener Habitats benötigt werden. Organismengruppen mit hoher Ausbreitungsfähigkeit, wie z.B. die Uferlaufkäfer, können als Pionierbesiedler gelten. Einige aquatische Gruppen hingegen benötigen aufgrund ihrer geringeren Ausbreitungsfähigkeit und den Einfluss vielfältiger Stressoren längere Zeiträume, um renaturierte Abschnitte zu erreichen. Oft werden schnelle Erfolge von Renaturierungsmaßnahmen auf aquatische Organismengruppen erwartet, die sich jedoch nur selten zeigen. Dementsprechend ist es wichtig, Bewusstsein für den Faktor Zeit zu schaffen und renaturierte Abschnitte über längere Zeiträume zu untersuchen.

Darüber hinaus beeinflusst das vorherrschende Abflussregime eines Gewässers die Entwicklung von renaturierten Abschnitten kurz- und langfristig. Im Fall von Mittelgebirgsflüssen, die natürlicherweise durch eine hohe Sedimentdynamik und damit langfristig durch einen Wechsel von Verjüngung und Sukzession charakterisiert sind, kann das Fehlen von Hochwasser in mehreren aufeinanderfolgenden Jahren zu einer zeitweise verringerten Habitatdiversität im Gewässer und der Aue führen. Werden die Untersuchungen von Renaturierungseffekten in dieser Zeit durchgeführt, besteht die Gefahr, dass eine Renaturierung aufgrund zunehmender Sukzessionsprozesse als erfolglos bezeichnet wird. Gerade für politische Entscheidungsträger und Gewässerbeauftragte spielt der potenzielle Erfolg oder Misserfolg einer Renaturierungsmaßnahme im Hinblick auf die zu tragenden Kosten für die Durchführung einer Maßnahme eine wichtige Rolle. Dementsprechend steigt das Interesse nach einem standardisierten Verfahren zur Erfolgskontrolle von Renaturierungen. Für aquatische Organismengruppen wurde dies bereits entwickelt. Für Auen steht dies jedoch noch aus.

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Appendix

Appendices are available on the attached CD-ROM.

Appendices to chapter 3:

Appendix 1	Riparian mesohabitats in non-restored and restored sections
Appendix 2	Vegetation units in non-restored and restored sections
Appendix 3	Taxalists of floodplain vegetation in non-restored and restored sections, and description of recorded vegetation units
Appendix 4	Taxalists of carabid beetles in non-restored and restored sections

Appendices to chapter 4:

Appendix 5	Aquatic and riparian meso- and microhabitats in the Ruhr river sections
Appendix 6	Taxalists of aquatic organism groups (benthic invertebrates, fish, aquatic macrophytes) in the Ruhr river sections, and classification of aquatic macrophytes in growth forms
Appendix 7	Taxalists of riparian organism groups (carabid beetles, floodplain vegetation) in the Ruhr river sections

Appendices to chapter 5:

Appendix 8	Floodplain mesohabitats and aquatic microhabitats in the Lahn river sections
Appendix 9	Taxalists of benthic invertebrates, carabid beetles and floodplain vegetation in the Lahn river sections

Der Lebenslauf ist in der Online-Version aus Gründen des Datenschutzes nicht enthalten.

Erklärung:

Hiermit erkläre ich, gem. § 6 Abs. (2) f) der Promotionsordnung der Fakultäten für Biologie, Chemie und Mathematik zur Erlangung der Dr. rer. nat., dass ich das Arbeitsgebiet, dem das Thema „River restorations – morphological effects on colonization and succession of aquatic and riparian organism groups“ zuzuordnen ist, in Forschung und Lehre vertrete und den Antrag von Frau Kathrin Januschke befürworte und die Betreuung auch im Falle eines Weggangs, wenn nicht wichtige Gründe dem entgegenstehen, weiterführen werde.

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